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# Same Risk Area Case-study for Kattegat and Øresund. Appendix 2: Connectivity analysis—Methodology, results and interpretation

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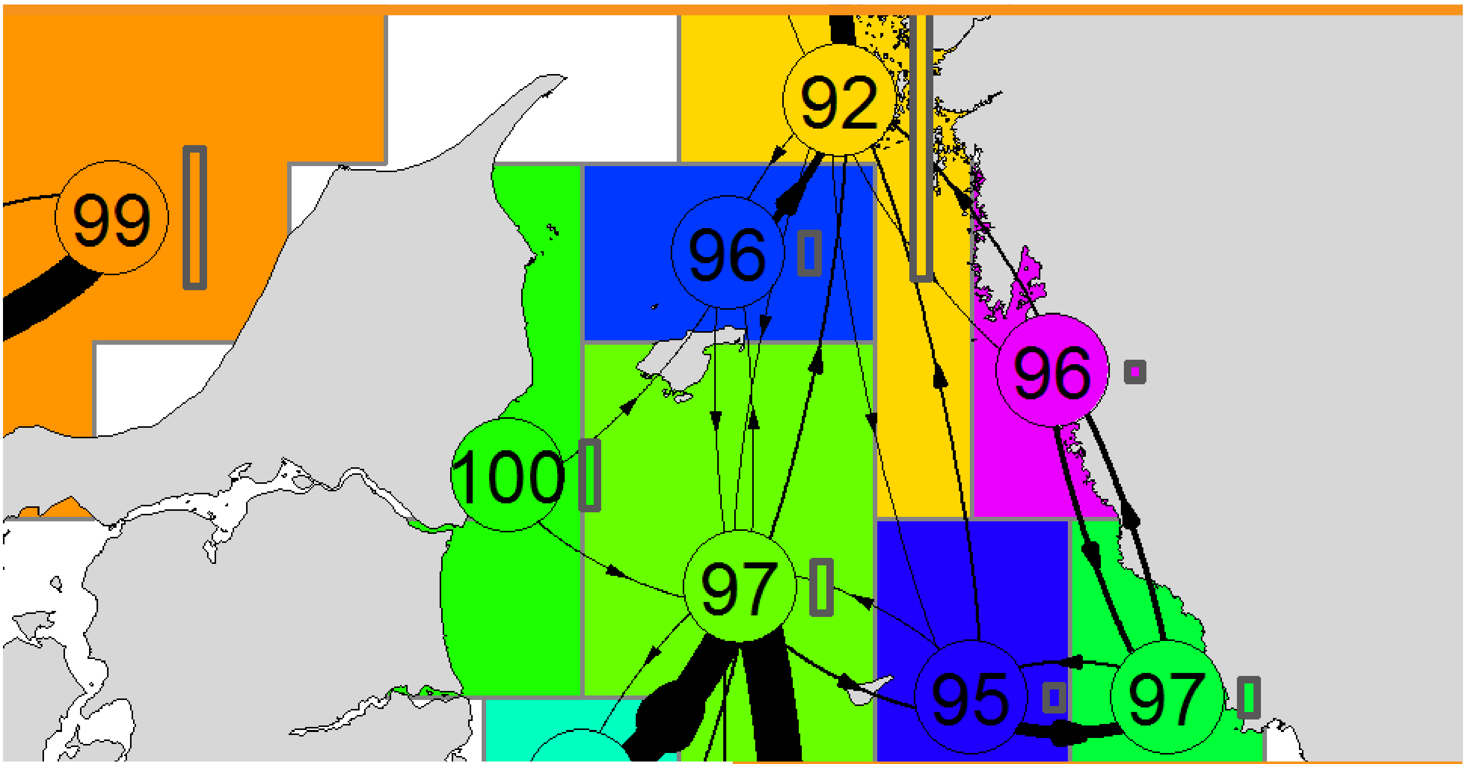
## Appendix 2: Connectivity analysis–Methodology, results and interpretation




**DTU Aqua report no. 335b-2018**

By Flemming Thorbjørn Hansen
and Asbjørn Christensen

DTU Aqua
National Institute of Aquatic Resources

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## Appendix 2: Connectivity analysis—Methodology, results and interpretation

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Flemming Thorbjørn Hansen and Asbjørn Christensen

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# 1 Introduction

This appendix 2 is an appendix to the report “SRA Case Study for Kattegat and Øresund. Section 2 in the appendix describes in detail the methodology applied for analyzing the natural dispersal of marine invasive species in the Kattegat and Øresund region. Section 3 presents the results of the analysis for each species considered in the case study and how the interpretation of results. Additional results supporting the interpretation of results are available in appendix 3. In section 4 we present additional relevant data available in the literature.

# 2 Methodology

## 2.1 Hydrographic data

Data on ocean current speed and direction, water temperature and salinity were extracted from a hydrographic dataset generated by the HBM model for the North Sea, Skagerrak, Kattegat, Inner Danish Straits and the Baltic Sea (for details: Berg and Poulsen 2012). The model uses a nested horizontal grid with a grid resolution of 3 nautical miles (~ 5.6 km’s) in the North Sea and Skagerrak and 0.5 nautical miles (~0.9 km’s) in the Kattegat, Inner Danish Straits and the Western Baltic Sea (Figure 1). The vertical resolution is 50 layers in the North Sea and 52 layers in transition zone between the North Sea and the Baltic Sea including the Kattegat, the Inner Danish Straits and the Western Baltic Sea. All values are stored as daily means.

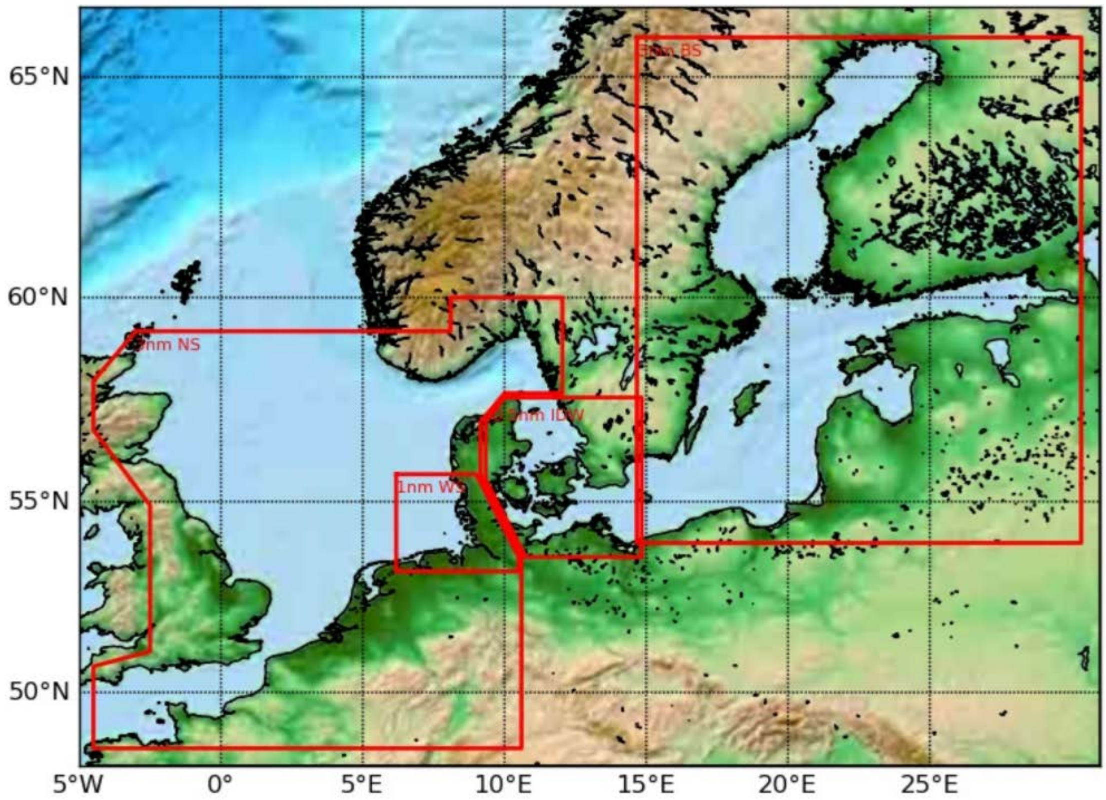



**Figure 1. The coverage, nesting and spatial resolution of the HBM model used as the hydrographic data source for the larval dispersal simulation (figure from Berg and Poulsen 2012).**

Three hydrographic years (2005, 2010 and 2012) based on the North Atlantic Oscillation (NAO) index were selected to represent different years with a neutral, a positive and a negative NAO index (Figure 2). The NAO influences the atmospheric variables such as wind speed, direction, air pressure and temperature, which in turn exert strong forcing on the ocean leading to changes in the temperature and salinity characteristics of the water (Drinkwater et al. 2003). Chen and Hellstrom (1999) studied the seasonal and regional atmospheric temperature anomalies in Sweden during the period 1861-1994 and found that the NAO index has an important effect on the regional Swedish temperature on the monthly and inter-annual scales. Correlation between monthly temperatures and NAO index were strongest during autumn and winter and weaker during summer months. Stramska and Białogrodzka (2015) studied the sea surface temperature (SST) in the Baltic Sean and found that the inter-annual SST variability in the Baltic Sea to be significantly correlated with the NAO index in the winter.

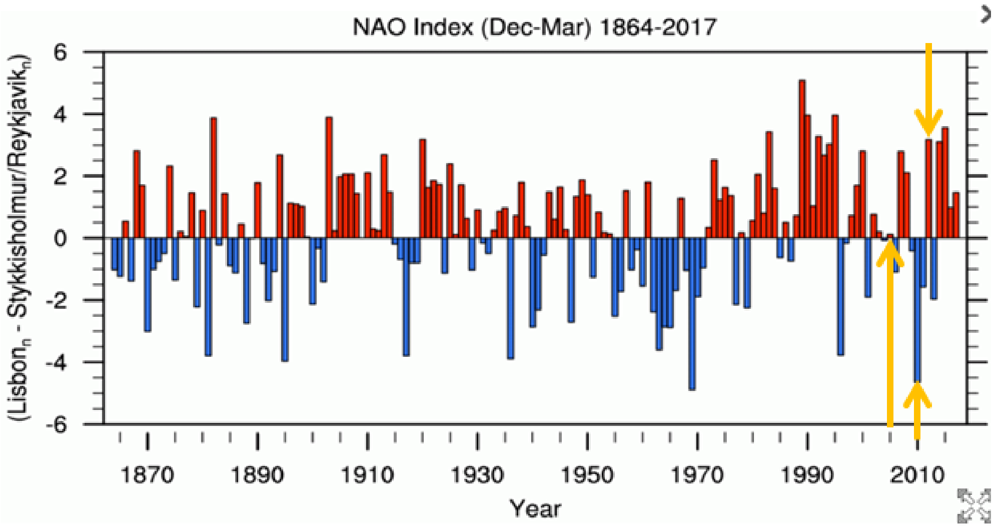



**Figure 2. The diagram shows the NAO index since 1860. Reference: Hurrell, J & National Center for Atmospheric Research Staff (Eds.). Arrows indicate the 3 selected years 2005, 2010 and 2012 representing neutral, a negative and a positive year.**

Thus, any hydrographic differences between years due to differences in the NAO index that may affect larval dispersal patterns is expected to occur primarily in species with spawning seasons starting in late winter or early spring and/or extending into the late autumn month.

## 2.2 Larval dispersal modelling

### 2.2.1 Agent-based model

The computational component of the SRAAM tool used for larval dispersal modelling and connectivity analysis (Hansen and Christensen 2018) consists of an agent-based modelling library (IBMlib) which is a freeware developed by DTU Aqua (Christensen 2008, Christensen et al. In review). The IBMlib implementation in the SRAAM tool supports a number of larval behaviors and parameters important for predicting larval dispersal. The larval behavior parameters and inputs used in the larval dispersal modelling for the SRA Case study for Kattegat and Øresund include:

- Pelagic larval duration (PLD)
- Dispersal depth interval
- Spawning start and end
- Spawning and settling habitat
- Vertical dispersion
- Horizontal dispersion

Some larval behavior mechanisms that may be important for predicting larval dispersal for some species were not included because none or very limited data was available. These include:

- Active settling
- Diurnal or tidal vertical migration behavior

Active settling refers to larvae among some species achieving settling competency at a certain age after which they are able to “sense” if the habitat is suitable for settling and such behavior has been reported for many species. Vertical migration of pelagic larvae, either diurnal or an optimization to environmental conditions such as tidal drift, predation avoidance or resource availability, is a well know mechanism for some pelagic larvae (e.g. Rodrigues et al. 1993). During the larval dispersal simulation, the IBMlib keeps track of start and end positions of each simulated larvae and minimum and maximum values of salinity and temperature experienced during the pelagic stage. These are used as input to connectivity analysis to construct connectivity matrices and to account for environmental tolerances, see later.

### 2.2.2 Parameters settings

**Pelagic larval duration**
The pelagic larval duration values reported for a species are often specified as a minimum and maximum range. In the larval dispersal simulation, we used the minimum values, knowing that minimum values are often associated with optimal temperature conditions and an increase in the PLD with decreasing temperatures (Hoegh-Guldberg and Pearse 1995). In case of a large range between the minimum and maximum PLD values this has must be considered in the interpretation of results.

**Spawning start and end**
Information on spawning start and end for most species are typically described as start and end month of the year and with a reference to specific locations. We use these start and end months as input to the larvae dispersal simulations interpreting the start month as the first day of the month and the end month as the last day of that month. In practice the water temperature regime characterizing an area are often determining the onset of spawning either by an exceedance of a temperature threshold or temperature days. Neither is included in the currents analysis explicitly in the modelling approach, however, knowledge on temperature tolerances of larval and adult live stages will be considered in the interpretation of results.

**Dispersal depth**
Very limited data exists on the vertical distribution of pelagic larvae of benthic invertebrate during larval dispersal in general and for MIS specifically. A recent study by Corell et al. (2012) investigated the vertical distribution of pelagic larvae of shallow water marine and estuarine benthic invertebrates and fish in the Baltic sea and found large variability across taxonomic groups and a none random correlation with depth. Most taxonomic groups of species had their primary abundance at depth intervals of 0 – 10, 10 – 20 and 20 – 50 meters depth, with polinoid polychaetes as an exception with highest abundances between 30 – 190 meters. Due to the lack of species-specific data on larval drift depths for marine invasive species, we use a constant dispersal depth of 0 – 40 meter. In more shallow areas, the water depth limits the depth distribution. In Kattegat and Øresund, the majority of the area has a water depth less than 40 m.

**Vertical dispersion**

To ensure a random distribution across this depth interval we applied a constant vertical dispersion of 0.001 $m^2/s$.

**Horizontal dispersion**

Horizontal dispersion is included primary to reflect the unresolved hydrodynamics of the hydrographic data at scales smaller than the spatial resolution of the model. The horizontal dispersion is set to 10 $m^2/s$.

### 2.2.3 Habitat maps

Habitat maps for each species were created based on information on species-specific preference of seabed substrate, depth distribution and adult life-stages salinity tolerances (Table 1 in the main report). Seabed substrate distribution was *derived from data that is made available under the European Marine Observation Data Network (EMODNET) Seabed Habitats project (www.emodnet-seabedhabitats.eu), funded by the European Commission's Directorate-General for Maritime Affairs and Fisheries (DG MARE).* EMODNET substrate data classification was regrouped into 3 main categories "Mud", "Sand" and "Hard substrate", Table 2. In both the "hard" substrate and "Sand" categories, we included "Mixed Sediments" and "Coarse Sediments" to reflect transition between the two habitat types.

**Table 1. EMODNET seabed substrate data classified into 3 main categories "Mud", "Sand" and "Hard substrate".**

| Mud | Sand | Hard |
|---|---|---|
| Fine mud<br>Mud to muddy sand<br>Sandy mud to Muddy sand<br>Muddy Sand<br>Sandy Mud | Sand<br>Coarse Sediment<br>Mixed Sediment | Rock or Other hard substrata<br>Coarse Sediment<br>Mixed sediments |

Data on water depth was based on GEBCO bathymetry data set (IOC, IHO and BODC 2003). Data on salinity was based on the hydrographic data from the HBM model by extracting minimum and maximum values of salinity from the bottom layer of the computational grid and for each year 2005, 2010 and 2012. Data extraction was done using a 0.1 degree grid and interpolated to a 0.025 degree raster using the IDW interpolation routine available in ArcGIS. For each raster grid cell the mean of the three years of minimum salinity (S-min) and maximum salinity (S-max) was calculated and applied for delimiting the habitats according to the minimum and maximum salinity tolerance thresholds found in the literature (Table 1 in the main report).

### 2.2.4 Simulation setup

The spatial extend of the larval dispersal simulations for each species were setup for a gross area extending 8-14 degree east, and 54–60 degrees north (Figure 2), to include not only the study area of Kattegat and Øresund, but also including the adjacent areas considered to affect population connectivity analysis outputs. The adjacent areas include the Skagerrak, the Inner Danish Straits and the western part of the Baltic Sea (Figure 2). The setup for each species and for each year included 200 000 agents distributed randomly in space within the areal coverage of the species habitat map, and uniform randomly in time within the spawning period.  We used a time step of 1800 seconds. To test the robustness of the connectivity analysis results sensitivity analysis were done by repeating all simulation with a reduced number of agents corresponding to 50 000 agents per species per year. To test for sensitivity to dispersal depth all simulations for 2005 were repeated with dispersal depth set to 0-15 m.

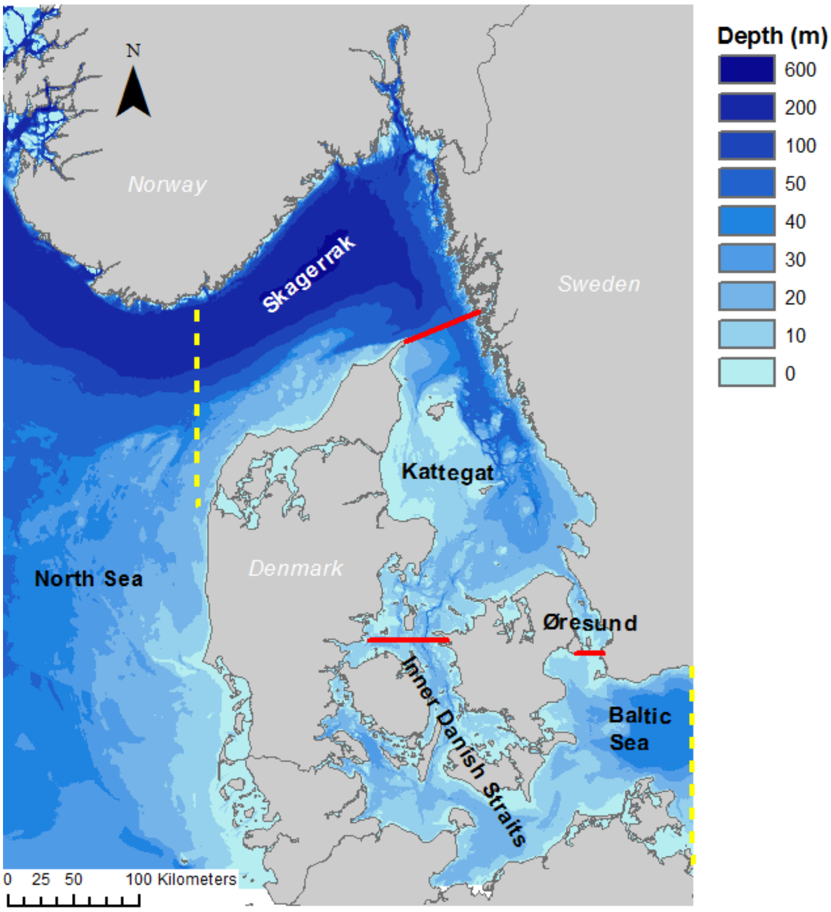



**Figure 3. The figure shows the transition zone between the North Sea and the western Baltic Sea including Skagerrak, Kattegat, Øresund and the Inner Danish Straits. Red lines indicate the outer boundary of the Kattegat and Øresund region. Yellow dotted lines indicate the extended area for which the larval dispersal model was setup. Blue color legend shows depth intervals based on the GEBCO bathymetry dataset (IOC, IHO and BODC 2003).**

## 2.3 Connectivity analysis

All data analyses were carried out using the statistical and data analysis software R (R Core team 2013). The connectivity analyses were carried out using a sub-division of the gross area into a regular grid of 20 x 20 corresponding to a spatial resolution of 0.3 degree in both the latitudinal and longitudinal direction, in the following referred to as the connectivity grid. Prior to populating the connectivity adjacency matrix the larval dispersal results were queried to include only agents with an end position within the species-specific habitat map. In addition, agents exposed to critical salinity levels outside the larval salinity tolerance were not included. Consequently, depending on the extent and coverage of the habitat, the salinity tolerance and PLD, the final number of agents included in the connectivity analysis varies considerably between species. The connectivity adjacency matrices and the derived connectivity probability matrices were prepared for each species and for each year to identify any differences in connectivity patterns between years, and finally lumped into one matrix for each species representing all years. Hydrographic regions were delineated using cluster analyses each cluster representing assemblies of sub-areas (grid-cells in the 20x20-connectivity grid) where the connectivity between sub-areas within the clusters is high, and where the connectivity to neighboring clusters is low.  Here we use the clustering method “Infomap” (Rosvall and Bergstrom 2008) available in the R package “igraph”. The Infomap method is based on information theory principles and has been used recently to delineate hydrographic regions in the Mediterranean (Vincent et al. 2014). The use of Infomap requires that the connectivity probability matrix is converted into a graph (i.e. as in the context of Graph Theory) where graph nodes represent each sub-area in the connectivity grid, and where pairwise connectivity probabilities are translated into weights of graph edges between nodes in a directed graph. Here a “directed” graph refers to the connectivity probability from A to B may be different from the connectivity probability from B to A.

The hydrographic regions delineation was done base on an assumption of multiple generation stepping stone dispersal using the estimated number of generations within a 5 year period and assuming a between generation survival rate of 10% . In practice the connectivity probability matrices where multiplied by itself a number of time corresponding to the number of generations and adjusted to the between generations survival. The inclusion of multiple generation dispersal as a basis for hydrographic regions delineation is a highly theoretical approach that predicts the dispersal potential rather than the actual dispersal capability and succession of marine invasive species. Many other factors potentially affect the success of a species to colonize an area, which is not considered explicitly in this approach.

The output of the connectivity analysis for each species is a number of maps showing the hydrographic regions identified from the cluster analysis of the connectivity probability matrices (Figure 4).

**Hydrographic region outline**
Each hydrographic region is represented by a unique color. The exact border between regions is determined by the resolution of the connectivity grid applied. Here we use a 20x20 grid.

**IBMlib filename**
The IBMlib result filename prefix is shown in the top part of the map with information on species name, simulation year, and number of agents included in the simulation per year. Notice that the number of agents used in connectivity analysis and for delineating hydrographic regions may be much lower depending on the agent filters applied, e.g. settling habitat, salinity tolerances and the proportion of agents that are exported out of the study area (~extension of the connectivity grid) due to ocean currents and the duration of pelagic stages. The term “All” included in the filename prefix indicates that the delineated hydrographic regions are based on the sum of all three years 2005, 2010 and 2012.

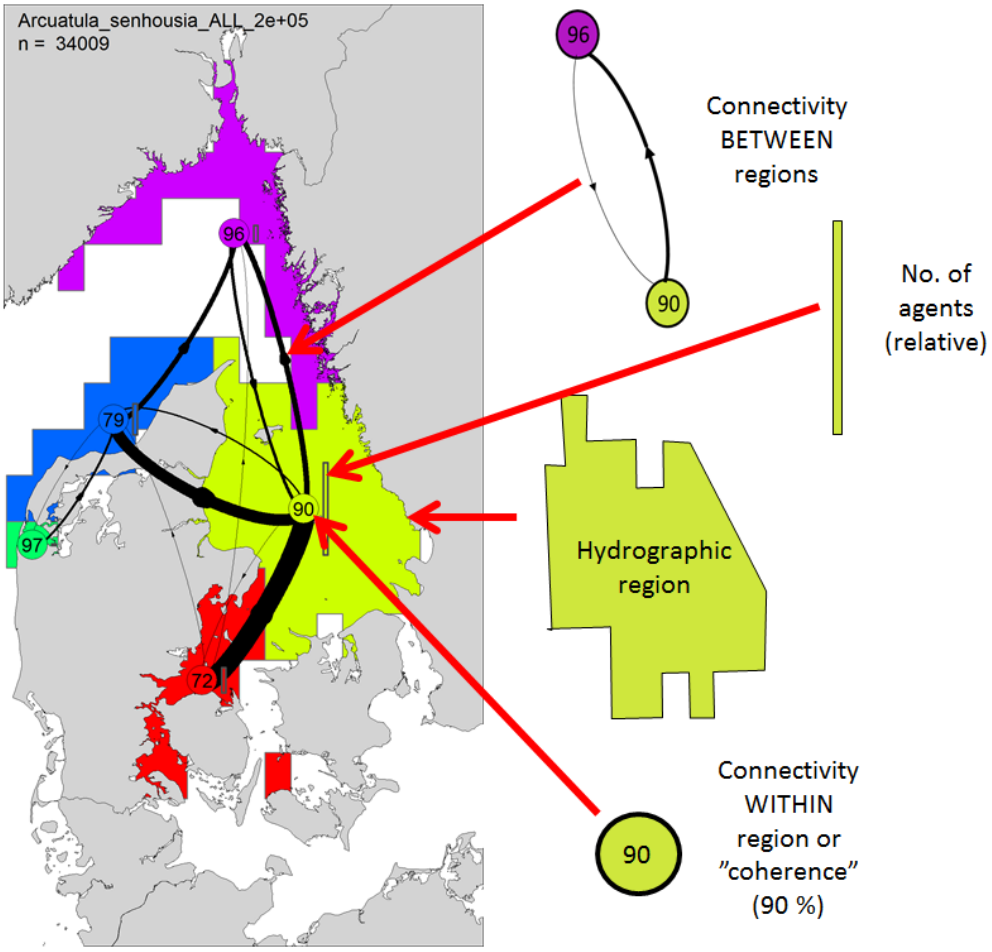



**Figure 4. Example of a graph plot representing the outline of hydrographic regions (individual colored polygons) identified for the species *Arcuatula senhousia* based on larval dispersal simulation results for ALL three years (2005, 2010 and 2012) using an initial number of 200 000 agents per year, i.e. a total of 600 000 agents. The number of agents included in the connectivity analysis is 34 009 (n). Bars represent the number of agents supporting the delineation of each individual region relative to the region with the largest number of agents. The WITHIN region connectivity for each region is represented by node values (circles) representing the percentage of agents with an initial position in each region that end up in the same region. The BETWEEN regions connectivities are indicated by arrows representing the direction of the connectivities and arrow thicknesses representing the relative magnitude of the connectivity (max thickness set to 17% after which it remains unchanged). White areas represent areas outside the larval dispersal extend due to lack of suitable habitat and/or due to unfavorable salinity conditions exceeding the larval salinity tolerance limit. Grey areas are land masses.**

### Within region connectivity

The WITHIN region connectivity, also referred to as "coherence" is shown in a circle (~ the geometrical centroid of the hydrographic region polygon) with the same color as the region it belongs to. The value represents the percentage of the number of agents with an initial position within the region that ends up in the same region, also referred to as coherence. The remaining percentages of agents are exported to the other regions. Notice that the percentage only represents the fraction of the total number of agents with an initial position within the region which ends up successfully within a suitable habitat in the region itself or one of the other regions, and which are not exposed to salinity conditions during drift that exceeds the larval salinity tolerance thresholds.

**Between regions connectivity**
Between regions connectivities are shown as arrows between hydrographic region centroids (~circles) arrow heads indicating the direction of the connectivity and the magnitude represented by arrow line thickness. A maximum constant thickness is applied to connectivities equal to or larger than 17 %. If no arrow is included between regions in one or both directions no connectivity has been detected. The interpretation of the BETWEEN regions connectivities are critical for the SRA risk assessment and whether a connectivity is interpreted as low or high. The magnitude and directions of the connectivities may be evaluated in combination with knowledge on species life-history characteristics such as:

- Small or large reproductive output
- High or low recruitment survival rate
- Whether the region is at the center or at the edge of its expected distribution (i.e. available habitats, salinity tolerance, temperature tolerance, etc.)
- The degree of uncertainties to the above and to the assumptions applied in the dispersal simulation (e.g. hydrography, spawning time, PLD, habitat, drift depth, etc.)

**Number of agents 'n'**
The total number of agents included in connectivity analysis is shown below the filename prefix at the top of the map. This number represents the total number of agents used in the hydrographic regions delineation AFTER the exclusion of agents settled outside suitable habitats, agents experiencing salinities conditions outside the salinity tolerance range of larval stages, and agents exported out of the study area. Because the number of agents are critical for achieving a robust and reliable result in terms of the hydrographic regions delineation, within, and between regions connectivities, it is important include information about the number of agents included in the connectivity analysis with an initial position within each region. The delineation of regions with a low number of agents may be more uncertain than the delineation of hydrographic regions with large number of agents.

**Bars**
The bars next to the circled number (= within region connectivity) indicate the proportion of the number of agents with an initial position inside the region relative to the number of agents of the region in the plot that has the largest number of agents with an initial position inside the region.

To supplement the interpretation of the connectivity from delineated hydrographic regions a number of maps for each species has been produced visualizing the upstream and downstream connectivity probabilities for 7 major harbors of Kattegat and Øresund including Frederikshavn, Gothenburg, Grenå, Varberg, Copenhagen, Helsingør and Helsingborg (Figure 5). The latter two are considered as one location due to the limitation in model resolution. Downstream connectivity represents the probability that an agent with the initial position in a subarea (e.g. close to Frederikshavn, Figure 5) ends up in any of the other subareas. Upstream connectivity probability represents the probability that an agent ending up in a sub-area (e.g. close to Frederikshavn, Figure 5) has a start position in each of the other sub-areas. Downstream and upstream connectivity maps have been generated for each species and for each of the major harbors in Kattegat and Øresund and based on larval dispersal modelling result lumped for all 3 years. Maps include both single generation and multiple generation (~5 years) upstream and downstream probability maps.

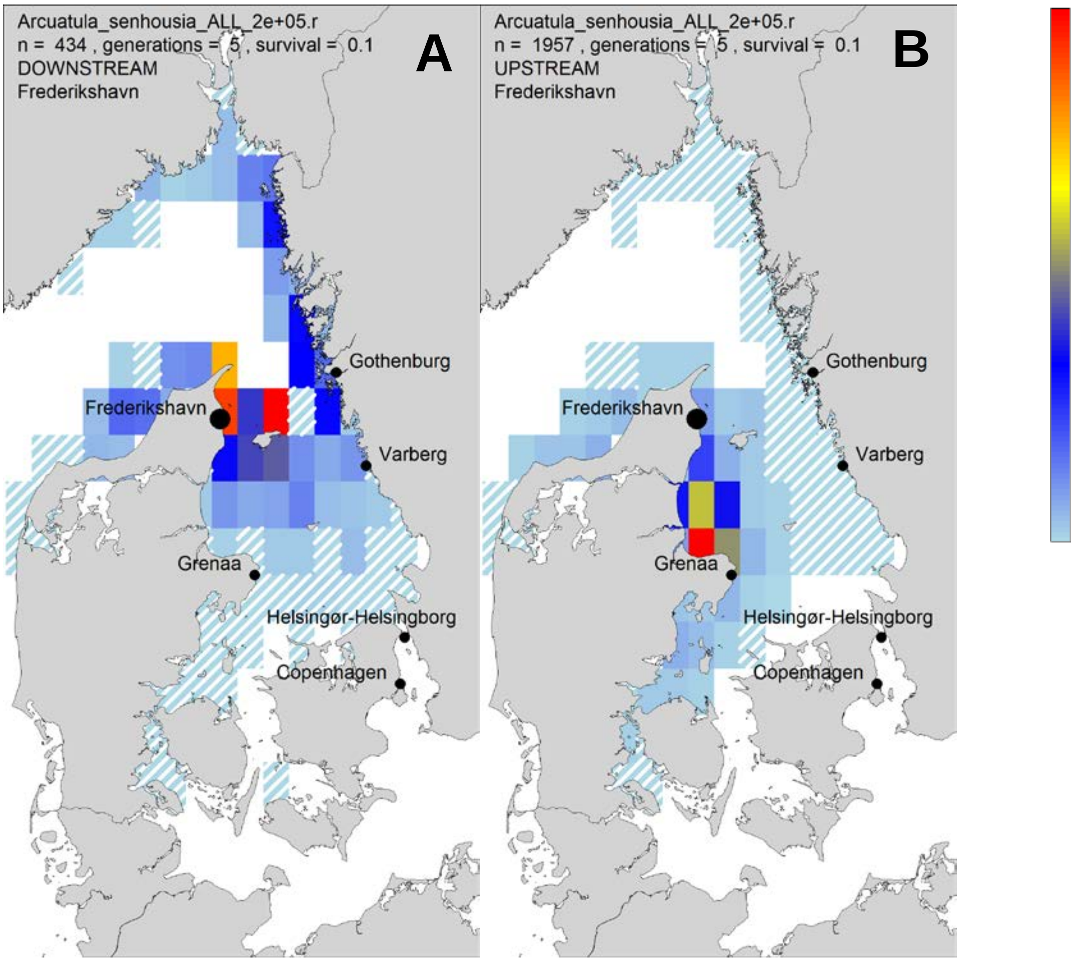



**Figure 5. Examples of downstream (A) and upstream (B) dispersal probability maps based on multiple generations dispersal (5 generations and 10 % survival between generations) for the harbor of Frederikshavn. Only agent successfully settled inside species habitats are included. Agents exposed to salinity levels outside the larval salinity tolerance thresholds are not included. Color legend is linear and relative to the largest probability value in each plot. Hatched light blue colors indicate dispersal probability less than 0.1 %. White areas are areas with dispersal probability of "0". Number of agents (n) included in the downstream and upstream probability plot is 434 and 1957 respectively.**

## 2.4 Interpretation of results

### 2.4.1 Conservatism of assumptions

The connectivity analysis is a theoretical and non-validated approach provided to give an estimate on the potential dispersal and connectivity in an area where species has not yet been introduced or where introduction may have occurred but with none or limited population consolidation locally. This potential is by no means synonymously with a risk assessment. Assumptions have to be considered carefully and the translation of each species-specific dispersal probabilities and hydrographic region delineations into a risk assessment estimate must be performed in concert with best available knowledge on species life history, invasion history, dispersal potential, and expert judgement and experience.

A number of issues need to be considered before evaluating the risk of a species being able to spread efficiently within an area. Some assumptions applied in the larvae dispersal simulations and in the connectivity analyses are conservative while others are non-conservative or liberal.

Non-conservative assumptions:

- Dispersal calculations are based on an ideal situation where each species are assumed to be evenly and numerously distributed in all suitable habitats within the region and in its vicinity. The early population stages of a newly introduced species will require time for a population to establish locally in competition with existing species, and this critical part of as successful population establishment is not considered in the connectivity analysis.

- Mortality is not included as a factor in the 1$^{st}$ generation dispersal; however, mortality is likely to correlate positively with PLD everything else being equal. Thus, the connectivity results for species with long PLD may be overestimated relative to species with shorter PLD. In addition, mortality is highly variable from species to species and knowledge is typically not available. The inclusion of high mortality rates in larvae dispersal simulations requires excessive number of agents and hence computational effort.

- Multigenerational dispersal assumes efficient stepping stone dispersal with a constant between-generations dispersal adjusted to include a 90% mortality per generation. Realized stepping stone dispersal depends on recruitment success from post-settled larvae to viable populations, which are not included in the model.

Conservative assumptions:

- The dispersal simulations are consistently using the smallest PLD value in the inspected range, thus for some species the PLD range is large and the dispersal probability (and distance) may be underestimated.

- Active settling is not included in the dispersal simulation. Active settling will increase the chance of simulated larvae settling on suitable habitat, and thus, ignoring active settling the connectivity may be underestimated, although the implication may be more complex underestimating short distance connectivities and overestimating connectivities at longer distances.

Other assumptions that can act both conservative and non-conservative:

- Reproductive output is not included explicitly in the dispersal simulation. Difference in reproductive output between species in nature may explain some of the difference in between-species dispersal potential and connectivity, along with other important life history traits and environmental tolerances that affect mortality.

### 2.4.2 Interpretation connectivity analysis results

With the assumptions and their implications for result interpretation in mind, connectivity analysis results for each species were evaluated one at the time, considering:

- **The dispersal potential** of the species expected in the Kattegat and Øresund region
- **The habitat maps** and how well habitats are expected to represent species habitat preferences
- **The robustness** of the larval dispersal simulation and the connectivity analysis results.

Points being considered are described in more details are outlined below.

**Dispersal potential**

The dispersal potential of the species expected specifically in the Kattegat and Øresund may consider the… :

- **Historic evidence** of the invasiveness potential.
- **Reproduction potential** including brood size and frequency, time-to-maturity, generations per year.
- **Larval survival** although information are typically not available.
- **PLD variability** in particular if the reported range of values is large.
- **Presence status** in the region, e.g. if the species has been recorded for decades still being relatively rare may indicate the species may not be invasive to the region.

**Habitat characteristics**

The habitat maps and the degree to which the habitat predicted for Kattegat and Øresund is representative for the species and its potential for supporting the species populations, may include consideration on:

- **Distribution and coverage**, e.g. small fragmented patches vs. large contiguous habitats.
- **Habitat representation** and if the habitat map is expected to represent good agreement with actual habitat? A number of habitats may not be adequately described such as hard substrate along shorelines including harbors, wave protections, biogenic reefs, mussel beds, stones or benthic vegetation.
- **Adult vs. "larvae settling habitat" discrepancies.** Adult habitat may differ from larval settling habitat. How does this affect the interpretation of results?
- **Salinity/temperature regime.** Are the habitat conditions in general optimal or suboptimal?

**Robustness of connectivity analysis results**

Robustness of simulation results here refers primarily to the credibility of the simulation results which can be critical if the number of agents included in the connectivity analysis is affecting the output. The considerations may include:

- **Number of agents.** Different or similar results when applying 50 000 and 200 000 agents respectively per simulation.
- **Between years differences** reflecting hydrographic inter-annual variations.

- **Fraction of agents** included in the connectivity analysis and for the individual hydrographic regions
- **Drift depth assumptions.** How these may have effects on the connectivity analysis results.

The results from the connectivity analysis interpretation for each species is summarized in a table using a simple 3 level scoring principle (Table 2) and considering the connectivity of the whole of Kattegat and Øresund and of five sub-divisions including southern, northern, eastern and western parts of Kattegat and the Øresund (Figure 6).

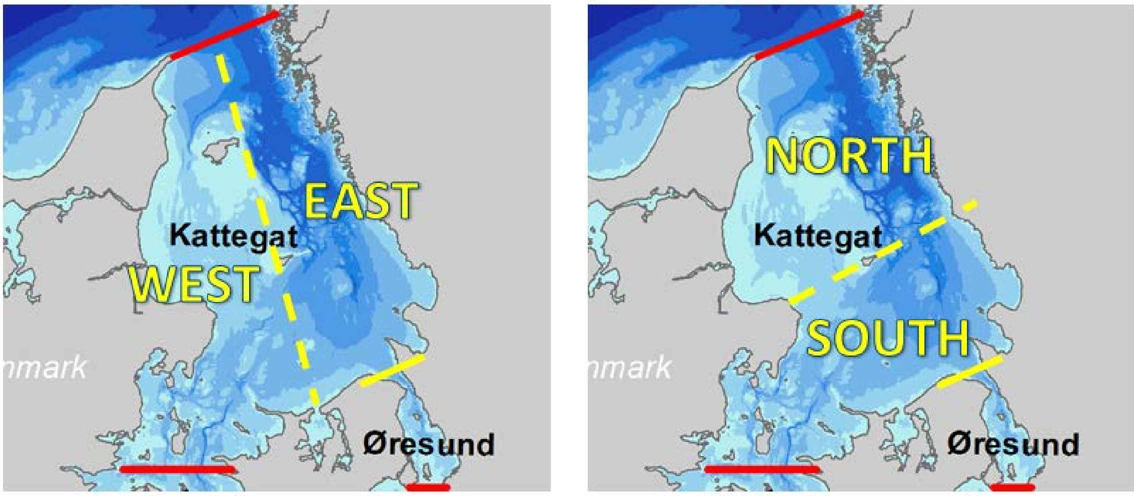



**Figure 6. The division of the Kattegat and the Øresund region into 5 subareas used for evaluating and interpretation of connectivity analysis results for each species: North, south, west and east Kattegat and Øresund. The subdivision is only approximate.**

While this subdivision should only be considered as approximate, it was chosen to provide a simplified overview of the connectivity analyses results and to identify which parts of Kattegat and Øresund where connectivity between Danish and Swedish marine areas and harbors may be critical.

**Table 2. Connectivity ratings ("no", "low" and "high" connectivity) evaluated for each species for the whole of Kattegat and Øresund (KØ) and for each sub-area (Figure 4) representing the North (N), South (S), East (E) and West (W) of Kattegat, and the Øresund (Ø). Additional ratings for the Kattegat and Øresund region as a whole include the "dispersal potential" of the species expected specifically for the region, the "habitat conditions" in terms for habitat representativeness of habitat map applied in the analysis and the "robustness" of the connectivity results. These are rated "high" (3), "medium"(2) and "low" (1). The presence status of the species in Kattegat and Øresund is also included dividing the species into "not registered" (-), "registered" (+) and "widely distributed" (++).**

| "...Species name..." | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 1,2,3 | | | | | |
| Habitat conditions | 1,2,3 | | | | | |
| Pressence status | - / + / ++ | | | | | |
| Robustness | 1,2,3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | | |
|---|---|---|---|---|
| (red) = No | 1 Low | - | = Not registerd |
| (yellow) = Low | 2 Medimu | + | = Registrered |
| (green) = high | 3 High | ++ | = Widely distributed |

The connectivity of each sub-area and the whole of Kattegat and Øresund are represented by three colors “green”, “yellow”, and “red” referring to “high”, “low” and “no” connectivity respectively. No color is used if the area is outside the expected larval dispersal range due to intolerance to experienced simulated salinities or absence of suitable habitat. Since the 5 minor areas are sub-areas of the Kattegat and Øresund the connectivity of the Kattegat and Øresund as a whole cannot be assigned a connectivity rating better than any of the individual sub-areas, i.e. if connectivity of southern Kattegat is “red”, the connectivity of the whole Kattegat and Øresund will also be assigned the color “red”. The presence status of the species in the Kattegat and Øresund region or in its close vicinity is included with 3 ratings: “widely distributed” (++), “registered” (+) and “not registered” (-). Additional ratings for the Kattegat and Øresund region as a whole presented in Table 2 include the “dispersal potential” of the species expected specifically for the region, the ”habitat conditions” in terms for habitat representativeness of habitat map applied in the analysis and the “robustness” of the connectivity results. These are rated “high” (3), “medium”(2) and “low” (1). Ratings from all species are summarized in the Risk Assessment section in the main report

# 3 Results


## 3.1 Arcuatula senhousia

### 3.1.1 Connectivity

The central region of Kattegat is identified as a well-connected hydrographic region ( ~ 90% coherence) delimited towards the south due to larvae intolerance to brackish conditions (Figure 7). A boundary towards the north is located close to the transition zone between Kattegat and Skagerrak. Connectivities towards the two hydrographic regions to the north include limited but mutual exchange of simulated agents. Sensitivity analysis carried out for 2012 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) shows similar results, however with some indication that there may be a limited connectivity in the east-west direction in the eastern parts of Kattegat.

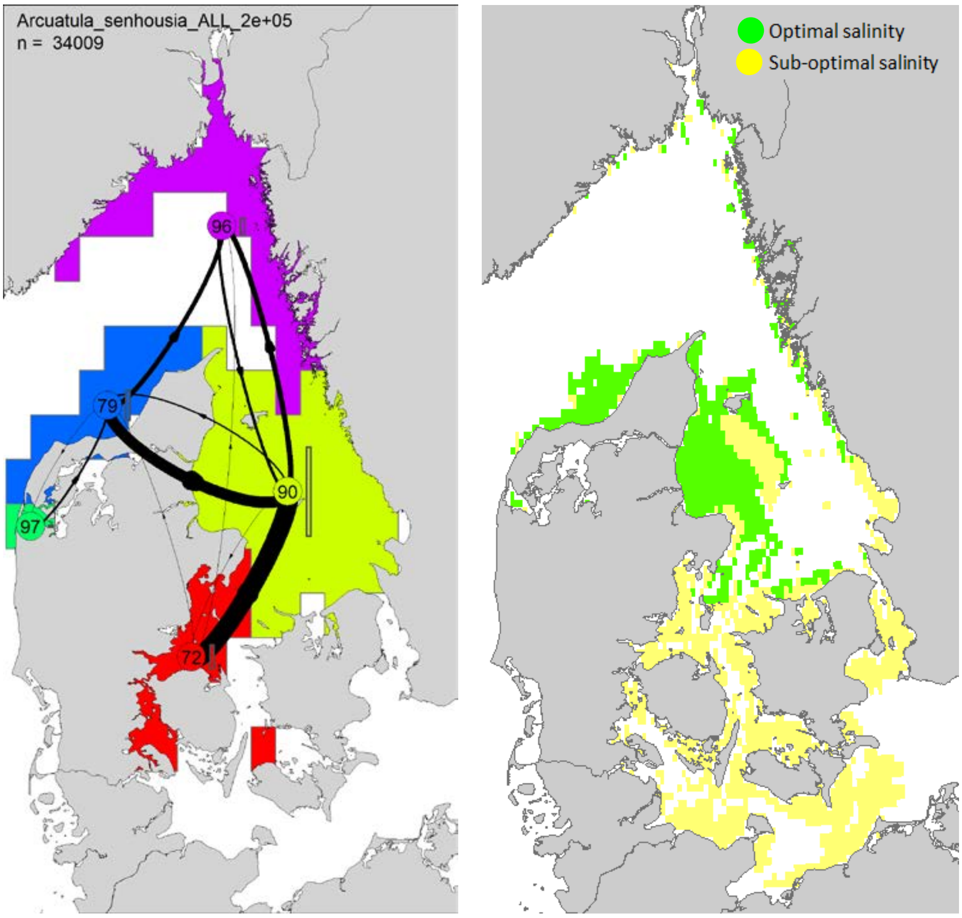



**Figure 7. Left: Hydrographic regions identified for *Arcuatula senhousia* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

Dispersal probability plots (Appendix 3) indicate that each of the 4 major harbors in the Kattegat (Grenå, Frederikshavn, Varberg and Gothenburg) are directly connected (i.e. within 1 generation) to at least one of the neighboring harbors. While there is a clear direct connectivity from west to east, the opposite direction may require multiple generations and stepping stone dispersal. The harbors of Copenhagen, Helsingør and Helsingborg lie outside the larval salinity tolerance limits.

### 3.1.2 Robustness of results

In total 34 009 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Very similar results were found for individual years. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) show some differences due to critical levels of agents used in the connectivity analysis for each year, however, he overall patterns were more or less preserved.  Thus, the analysis results are considered robust.

### 3.1.3 Habitat characteristics

Habitats consist of large contiguous areas of the central, southwestern, and western parts of the Kattegat, while habitats along the west coast of Sweden are scarce and fragmented, and may potential limit the connectivity towards the north and west. Southern parts of the Kattegat lye well within habitats with sub-optimal adult salinity conditions. It is uncertain if the species can withstand sub-optimal conditions during shorter periods. Larval dispersal is expected to be limited towards the southeastern parts of Kattegat and Øresund where salinity conditions are critical. Temperature is the major limiting factor for this species where the minimum requirement for reproduction has been reported to be 22.5 $^{o}$C and the species are typically found in warmer regions. Thus, the species potential distribution in Kattegat and Øresund will be in association with cooling water outlets.

### 3.1.4 Natural Dispersal potential

According to www.cabi.org *A.* s*enhousia* is a broadcast spawner with a relatively high reproductive potential. In addition, in the current study we use the minimum value of reported PLD of 14 days while the maximum reported PLD is 55 days. Thus, the connectivity calculated presented here may be underestimated. While reproduction in Kattegat under natural conditions is unlikely, in theory the species may disperse between locations affected by cooling water outlet during warm summers, however this has not been documented.

### 3.1.5 Summary

All though the natural dispersal potential of *A. senhousia* is expected to cover the whole Kattegat, except for the most south-eastern parts of Kattegat and the Øresund, and with a existing however limited connectivity from east to west in the eastern parts of Kattegat, population may establish only in areas affected by cooling water outlet. Connectivity between such areas may be possible during warm summers but this is uncertain.

**Table 3. Connectivity ratings and species characteristics. For details on ratings descriptions see methodology section in this appendix.**

| Arcuatula senhousia | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| Colour | | Rating | | Status | |
|---|---|---|---|---|---|
| Red | = No | 1 | = Low | - | = Not registered |
| Yellow | = Low | 2 | = Medimum | + | = Registered |
| Green | = high | 3 | = High | ++ | = Widely distributed |

## 3.2 Asterias amurensis


### 3.2.1 Connectivity

The Kattegat and the Skagerrak is identified as a single well-connected hydrographic region ( ~ 100 % coherence) and agents from this region constitute the single largest proportion of agents included in the connectivity analysis (Figure 8). Towards the south-west, smaller regions with low within regions connectivities are identified primary due to larval intolerance to low salinities and very few simulated agents successfully settling within suitable habitats. The southern boundary due to larval intolerance to brackish conditions is located approximately at the entrance of the Inner Danish Straits. Sensitivity analysis carried out for 2012 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) shows almost identical results. Dispersal probability plots (Appendix 3) indicate that each of the 4 major harbors in the Kattegat (Grenå, Frederikshavn, Varberg and Gothenburg) are directly and in some cases very efficiently connected (i.e. within 1 generation) to at least one of the neighboring harbors across the Kattegat. The harbors of Copenhagen, Helsingør and Helsingborg lie outside the larval salinity tolerance limits.

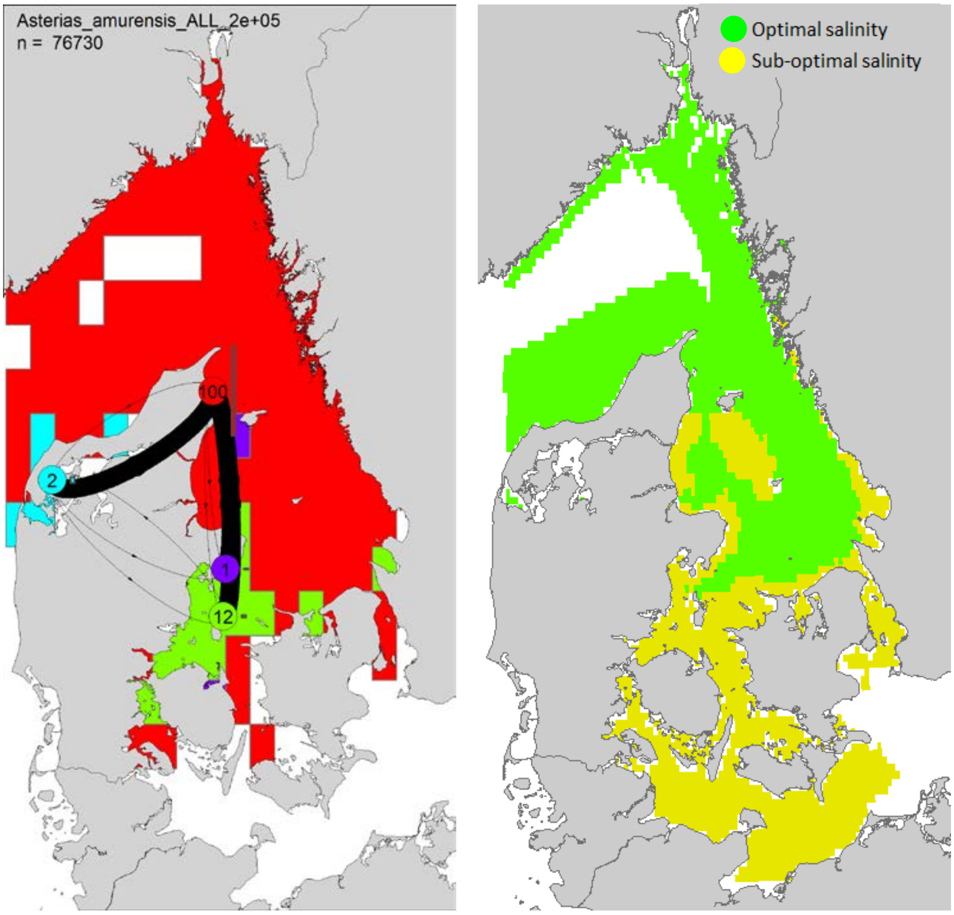



**Figure 8. Left: Hydrographic regions identified for *Asterias amurensis* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.2.2 Robustness of results

A total 76 730 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Hydrographic regions delineation for individual years (Appendix 3) show similar patterns with 2005 and 2010 indicating the whole area from the northern boundaries of the Inner Danish Straits and towards the North Sea being one big well-connected area. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year for 2005 (Appendix 3) also shows almost identical results. The identification of smaller regions in the south-eastern Kattegat with weak coherences is a result caused by a combination of the very high PLD value (41 days) resulting in long dispersal distances and larval intolerance to brackish conditions in the south-eastern parts of Kattegat reducing the successful larval settlement to very low numbers. The analysis results are considered robust.

### 3.2.3 Habitat characteristics

Habitats consist of large contiguous areas of the entire Kattegat and Øresund, and most of the habitats are within optimal conditions for adult *A. amurensis,* except for the southern parts of the Kattegat, Øresund and the shallow coastal areas of Kattegat. These areas are expected to be subject to temporal exposures of critical lower salinity levels. Adult *A. amurensis* exposed to salinities of 18 PSU and below for several days may induce mortality (Kashenko 2002). Some ability to recover depends on the duration and extent of exposure to critical salinity levels. Habitat conditions in Kattegat are expected to be suitable for supporting population connectivity in general, while in Øresund this is more questionable.

### 3.2.4 Natural Dispersal potential

According to www.cabi.org female *A. amurensis* is capable of carrying up to 20 million eggs and must be considered highly invasive supporting “bust and boom” cycles reaching high abundances if conditions are optimal. In addition, in the current study we use the minimum value of reported PLD of 41 days while the maximum reported PLD is 120 days. Thus, the connectivity calculated presented here may be underestimated. Temperature is expected to be close to optimal for both adult and larval life stages.

### 3.2.5 Summary

The natural dispersal potential of *A. amurensis* is expected to be very efficient in most of Kattegat. Eventual temporary population depletions due to adults exposed to critical salinities can rapidly be replaced by reproductive outcome of the specimens located in more saline habitats of Kattegat. The Øresund is considered outside the salinity regime tolerated by larvae, while salinity conditions may limit the successful larval settlement in the southwestern parts of Kattegat.

**Table 4. Connectivity ratings and species characteristics for *A. amurensis*. For details on ratings descriptions see methodology section in this appendix.**

| Asterias amurensis | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | |
|---|---|---|
| = No | 1 = Low | - = Not registered |
| = Low | 2 = Medimum | + = Registered |
| = high | 3 = High | ++ = Widely distributed |

## 3.3 Austrominius modestus


### 3.3.1 Connectivity

One region is identified supporting population connectivities of *Austrominius modestus* including the Norwegian and Swedish shores of Skagerrak, and in the coastal areas around Gothenburg (Figure 9). The expected absence of *A. modestus* in remaining parts of Kattegat and Øresund is caused primary by the larval intolerance to brackish conditions towards the south and the very limited and fragmented presence of suitable hard substrate habitats in 0-5 meters depth included in the analysis. Results from individual years (2005, 2010 and 2012) show the same southward boundary of larval dispersal. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 m and 15 m (Appendix 3) shows identical results. Dispersal probability maps indicate that only one of the major harbors, Gothenburg, may support interconnected populations *of A. modestus* with limited potential for larval dispersal towards the north. Although the 3 other major harbors in Kattegat (Grenå, Frederikshavn and Varberg) and surroundings may support *A. modestus* populations, simulated dispersal between harbors  are limited by larval intolerance to brackish water and the lack of suitable habitats identified for the western parts of Kattegat.

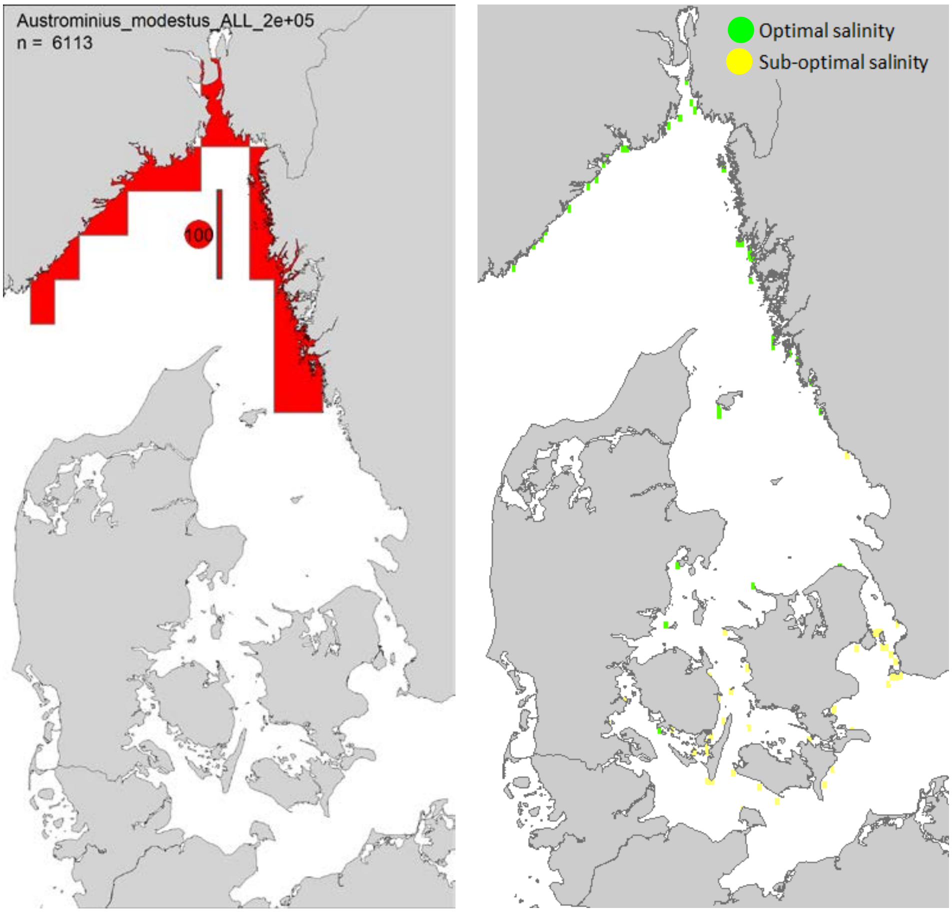



**Figure 9. Left: Hydrographic regions identified for *Austrominius modestus based on 3 years larval dispersal simulation (2005, 2010 and 2012).* Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.3.2 Robustness of results

In total 6 113 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Although this may be a critical number, hydrographic regions delineated for individual years show similar results (Appendix 3). In particular, the restriction of regions being located north of Gothenburg area is consistent among outputs. A major contribution to this pattern is the low larval salinity tolerance of 25 PSU, and the lack of suitable habitats in the central, southern, and western parts of Kattegat. Although the representativeness of the habitat map applied (see below) may be questionable, the analysis results given the habitat map applied are considered robust.

### 3.3.3 Habitat characteristics

Habitats suitable for *A. modestus* are limited to hard substrates in the littoral and sublittoral zone (0 – 5 m). The spatial resolution of EMODNET seabed habitat maps is 250 meters. Smaller scale fragments of hard substrate habitats including artificial substrates (shoreline constructions and protection) and scattered stones and boulders in the littoral zone originating from quaternary moraine deposits are not resolved. Mussel and oyster beds potential supporting populations of *A. modestus* are not included. Hence, the physical habitat for *A. modestus* may not be adequately described. Salinity minimum tolerance of the larval stage is set 25 PSU. According to www.cabi.org larval development can occur down to ca. 22 PSU. This may support population connectivities a bit further towards the south in Kattegat.

### 3.3.4 Natural Dispersal potential

According to www.cabi.org *A.modestus* has a relatively high reproductive potential producing several broods per year and a long spawning season. The reproductive potential is supported by successful introduction many places also in European waters. The relatively narrow range of reported PLD values (10 - 15 days) indicates that the extent and outline of the identified hydrographic regions are reasonable.  However, the probable inadequacy of data on habitat distribution makes the southward extent of potentially connected populations somewhat uncertain. No limitation due to temperature is expected.

### 3.3.5 Summary

The natural dispersal potential of *A. modestus* is expected to cover primarily the northeastern parts of Kattegat, with possible local populations further south and west toward the central Kattegat along coastal areas in relation to shoreline constructions and stones and boulders from quaternary moraine deposits. Despite limitations in habitat data, the natural dispersal is not expected to support larger hydrographic regions in the northern and central parts of Kattegat. Thus, Kattegat and Øresund region is expected to be outside the larval salinity tolerance range.

**Table 5. Connectivity ratings and species characteristics for *A. modestus*. For details on ratings descriptions see methodology section in this appendix.**

| Austrominius modestus | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 1 | | | | | |
| Habitat conditions | 1 | | | | | |
| Pressence status | 1 | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | | | |
|---|---|---|---|---|---|
| = No | 1 | = Low | - | = Not registered |
| = Low | 2 | = Medimum | + | = Registered |
| = high | 3 | = High | ++ | = Widely distributed |

## 3.4 Bugula neritina


### 3.4.1 Connectivity

Population connectivities of Bugula neritina (Figure 10) are highly limited by a short PLD (2 days) and highly fragmented hard substrate habitats. Habitat representativeness may be low due to data limitations, see below. Although suitable habitats are small and fragmented, the short PLD ensures that simulated larvae successfully settle on neighboring habitat patches. The delineated hydrographic regions are small, and the within dispersal connectivity of each region is generally high (coherence 92-100 % in the Kattegat and Øresund region) with limited exchange of simulated agents between regions, especially across the Kattegat. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) shows almost identical results, with indications that Øresund can be recognized as one connected region.

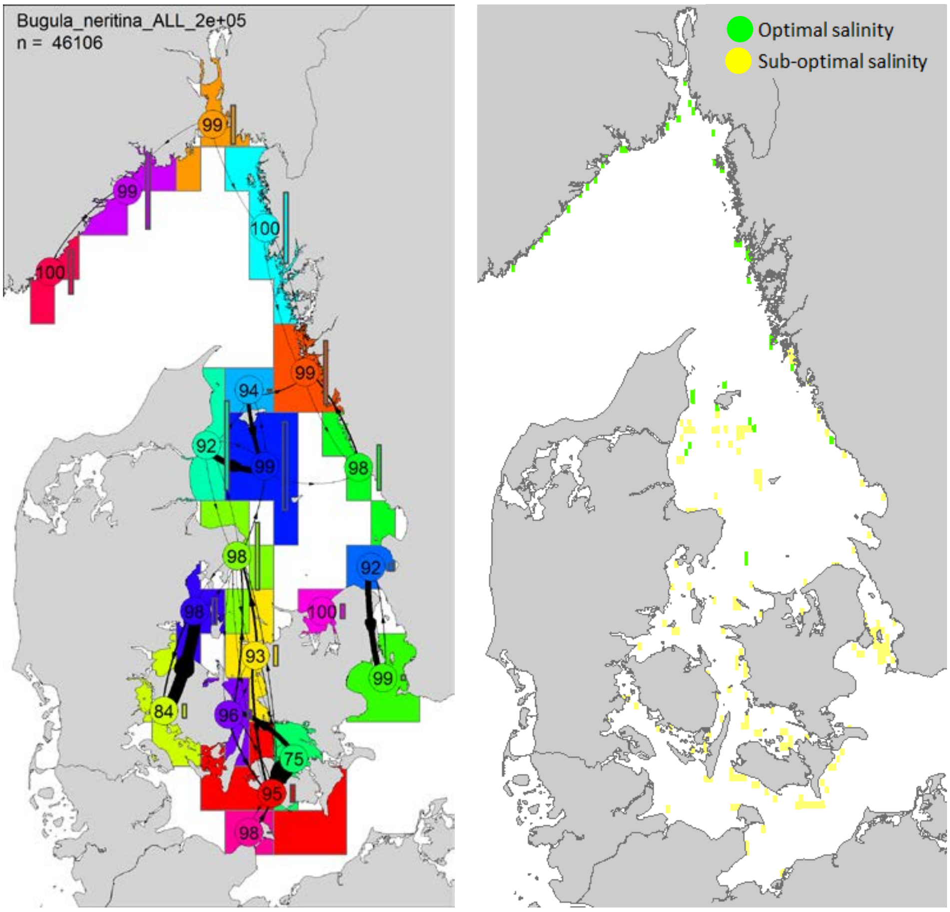



**Figure 10. Left: Hydrographic regions identified for *Bugula neritina* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

Comparisons between the different years (2005, 2010 and 2012) show almost identical results (Appendix 3). However, the year 2012 indicates that the Øresund may be well connected some years. Dispersal probability maps indicate that major harbors are not directly connected via 1st generation dispersal. Dispersal probability maps mimicking multiple generation dispersal (~ 5 years) indicate that limited bidirectional connectivity may exist between harbors along the west coast of Sweden, although the dispersal probability values are very low (< 0.1 %). No bidirectional connectivity across the Kattegat is identified. Throughout most of Kattegat and Øresund, adult salinity tolerance may be exceeded in shorter or longer periods

### 3.4.2 Robustness of results

In total 46 106 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Hydrographic regions delineation for individual years (Appendix 3) show very similar patterns. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) also show comparable results. Thus, the analysis results are considered robust.

### 3.4.3 Habitat characteristics

Habitats suitable for *B. neritina* are limited to hard substrates in the tidal, littoral and sublittoral zone (0 – 10 m). The spatial resolution of EMODNET seabed habitat maps is 250 meters. Smaller scale fragments of hard substrate habitats including artificial substrates (shoreline constructions and protection) and scattered stones and boulders in the littoral zone originating from quaternary moraine deposits are not resolved. According to www.cabi.org larvae of *B. neritina* also attach to organic material such as algae and other bryozoan colonies, as well as hard shells of oysters. These are not included in the habitat map. The physical habitat for *B. neritina* may not be adequately described.

### 3.4.4 Natural Dispersal potential

The invasion history of *B. neritina* in European waters is more than 100 years old, and current registrations in British, French and Dutch marine waters (www.cabi.org) indicate that the populations are established in numerous marinas and harbors. Some historic data suggests that populations of *B. neritina* has been frequently locally extinct with a believed correlation to winter temperatures during exceptional cold winters, however this may be uncertain (Ryland et al. 2011). Temperature is not expected to be a limiting factor for larvae. The species is a major fouling component and transition between harbors and marinas and is probably a single most important vector for the historic introduction and current distribution. Natural dispersal is limited due to very short PLD. For the larval dispersal simulation we used 2 days PLD (Keough 1989), however, shorter PLDs of 1 day or less may be expected if suitable habitat are found. Larvae are capable of active settling on suitable substrate this way reducing the PLD (Keough 1989). Although the habitat of *B. neritina* may not be adequately described the pattern of the hydrographic region delineation is not expected to change and alter conclusion.

### 3.4.5 Summary

The natural dispersal potential of *B. neritina* is expected to be very limited, except for the Øresund, and does not support larger hydrographic regions the Kattegat area. Since Øresund is located on the southern edge of predicted population extent due to population intolerance to brackish waters, it is uncertain if the population can establish here.

**Table 6. Connectivity ratings and species characteristics for *B. neritina*. For details on ratings descriptions see methodology section in this appendix.**

| Bugula neritina | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 1 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| Colour | | Rating | | Status | |
|---|---|---|---|---|---|
| Red | = No | 1 | = Low | - | = Not registered |
| Yellow | = Low | 2 | = Medimum | + | = Registered |
| Green | = high | 3 | = High | ++ | = Widely distributed |

## 3.5 Bugulina simplex


### 3.5.1 Connectivity

Population connectivities of *Bugulina simplex* (Figure 11) are highly limited by a short PLD (1days). Although suitable habitats are small and fragmented, the short PLD ensures that simulated larvae successfully settle on neighboring hard substrate habitats. Habitat representativeness may be low due to data limitations, see below. The size and extent of delineated hydrographic regions are small, with a slightly larger area in the central and western part of Kattegat as the only exception due to relatively dense habitat presence supporting multigenerational stepping stone dispersal. The within dispersal connectivity of each region is generally high (coherence between 90-100 % in the Kattegat and Øresund region) with limited exchange of simulated agents between neighboring regions, especially across the Kattegat. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) show almost identical results. Results for individual years (2005, 2010 and 2012) show between years variation in the southward boundary of larval dispersal due to intolerance to low salinity varying from a location in the center of Kattegat to a location in southern Øresund and Inner Danish Straits (Appendix 3).

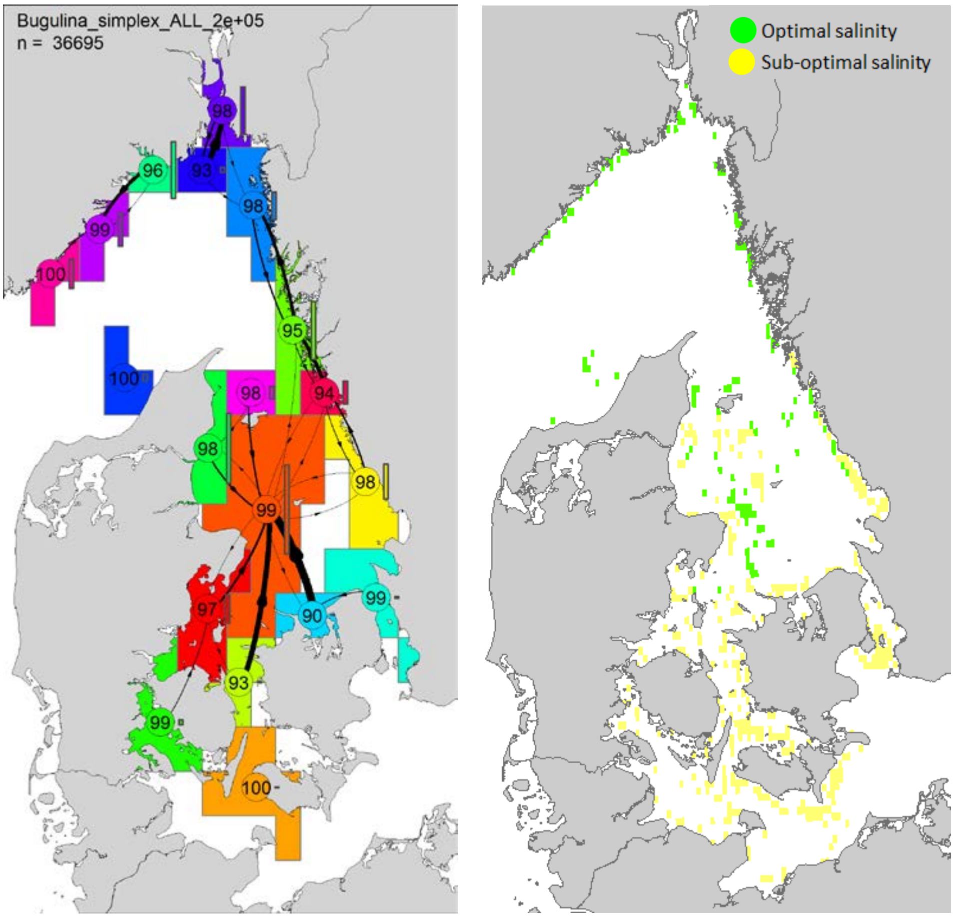



**Figure 11. Left: Hydrographic regions identified for *Bugulina simplex* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

Dispersal probability maps indicate that none of the major harbors are directly connected via 1st generation dispersal. Dispersal probability maps mimicking multiple generation dispersal indicate connectivity may exist between all major harbors (except the harbor of Copenhagen being outside the larval salinity tolerance range), however, the probability is very low (< 0.1 %).

### 3.5.2 Robustness of results

In total 36 695 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Hydrographic regions delineation for individual years (Appendix 3) show similar patterns of hydrographic regions, however with varying location of southward boundary of population extension due to larval intolerance to brackish conditions, where southern and southeastern Kattegat and Øresund may be at the limit of larvae salinity tolerance. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) also show comparable results. The comparable patterns of hydrographic regions across years besides from the southward extension of supported populations, indicates that the analysis results are considered robust.

### 3.5.3 Habitat characteristics

Habitats suitable for *B. simplex* are limited to hard substrates from the tidal zone down to 20 m. The spatial resolution of EMODNET seabed habitat maps is 250 meters. Smaller scale fragments of hard substrate habitats including artificial substrates (shoreline constructions and protection) and scattered stones and boulders in the littoral zone originating from quaternary moraine deposits are not resolved. According to www.invasions.si.edu larvae of *B. simplex* also attach to hard shells. Ryland (1959) referred to older studies that found *B. simplex* growing on eelgrass (*Zotera marina)*. These habitats are not included in the habitat map. Thus, the physical habitat for *B. simplex* may not be adequately described.

### 3.5.4 Natural Dispersal potential

According to www.invasions.si.edu the first recording of *B. simplex* was in Northern European waters was in 1957 in Wales. Since then it has been recorded as far north as far north as Shetland Islands. The limited PLD of 1 day or less strictly limits the natural dispersal of the species. Although the habitat of *B. simplex* may not be adequately described, the pattern of the hydrographic region delineation is not expected to change and alter conclusions. Temperature is not expected to be a limiting factor for larval dispersal.

### 3.5.5 Summary

The natural dispersal potential of *B. simplex* is expected to be very limited and not supporting larger hydrographic regions in the Kattegat. South-southeastern parts of Kattegat and the Øresund probably lie outside the potential extension of salinity tolerance of adults and larvae.

**Table 7. Connectivity ratings and species characteristics for *B. simplex*. For details on ratings descriptions see methodology section in this appendix.**

| Bugulina simplex | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 1 | | | | | |
| Habitat conditions | 1 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | |
|---|---|---|---|
| = No | 1 = Low | - | = Not registered |
| = Low | 2 = Medimum | + | = Registered |
| = high | 3 = High | ++ | = Widely distributed |

## 3.6 Callinectes sapidus


### 3.6.1 Connectivity

The central and northern parts of Kattegat and the Skagerrak are identified as one well-connected hydrographic region for *Callinectes sapidus* (coherence values of 100 %)(Figure 12). Connectivity towards the south is limited due to larvae intolerance to brackish conditions, which is also why the southwestern part of Kattegat is identified as one separate region with a unidirectional connectivity to towards the northeast and represented by a low number of agents in the analysis.

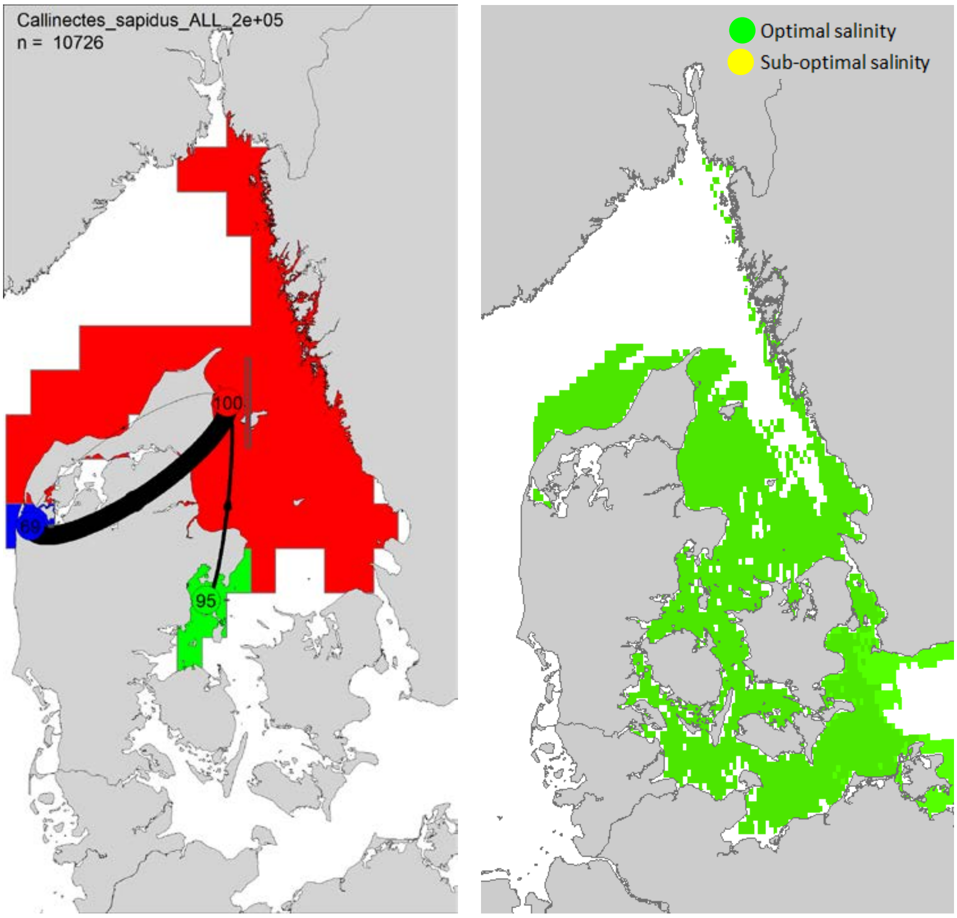



**Figure 12. Left: Hydrographic regions identified for *Callinectes sapidus* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

The low number of agents included in the connectivity analysis (10 726) despite the large habitat coverage is caused by a combination of larval intolerance to brackish conditions and long PLD of 31 days. The long PLD increases the likelihood of simulated larvae being exposed to critical salinity conditions, while larvae that remain within optimal salinity conditions may be exported towards the North Sea. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) show similar results with a less agents successfully settling in the in central Kattegat due to lower salinity in surface water originating from the Baltic Sea. Dispersal probability plots (Appendix 3) indicate that each of the 3 major harbors in the northern and eastern Kattegat (Frederikshavn, Gothenburg and Varberg) are more or less directly connected (i.e. within 1 generation) to the other two neighboring harbors. Harbors of Grenå, Copenhagen, Helsingør and Helsingborg lie outside the larval salinity tolerance limits.

### 3.6.2 Robustness of results

In total 10 726 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Despite the relative low number of agents per year (2005, 2010 and 2012)the delineation of hydrographic regions all show the northern Kattegat and Skagerrak as one well connected region with approximately the same southward region extension due to larval intolerance to low salinity (Appendix 3). Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) show similar results. The results in terms of hydrographic regions delineations are considered robust.

### 3.6.3 Habitat characteristics

Habitats suitable for *C. sapidus* cover large contiguous areas with no limitations in salinity tolerance of adult stages. Adults of *C. sapidus* are capable of inhabiting a large range of salinities from freshwater to marine condition. Adults of *C. sapidus* cable of swimming and migrating over large distances (>100 km) towards more saline conditions have been observed in estuaries during spawning season ensuring suitable conditions for larvae brackish water intolerance (e.g. Hench et al. 2004). Thus *C. sapidus* is probably capable of extending adult population into more brackish areas as adults. Also later post larvae stages are more salinity tolerant than larvae and may play a role in extending population outside the larvae tolerance limits. Survival is significantly reduced at temperatures lower than 5 degrees Temperature (Rome et al. 2005) where a hibernative state is induced. It is unknown if this is a potential limiting factor for establishment and succession of *C. sapidus* populations in Kattegat.

### 3.6.4 Natural Dispersal potential

According to the Danish EPA (Miljøstyrelsen 2017) *C. sapidus* was found the first time in Øresund in 1951 but the species has failed to establish in northern Europe, possibly due to temperature limitations and/or larval intolerance to low salinity. The species has not been registered in Swedish waters. Each female produces 2-6 millioner eggs and if conditions are optimal, the dispersal potential is high.

### 3.6.5 Summary

It is questionable if *C. sapidus* will be able to establish viable populations in Kattegat region if temperature is a limiting factor. In any case, larval intolerance to brackish water will limit larval dispersal to the central and northern parts of Kattegat including at least the three major harbors Grenå, Frederikshavn and Gothenburg where connectivity is expected to be high.

**Table 8. Connectivity ratings and species characteristics for *C. sapidus*. For details on ratings descriptions see methodology section in this appendix.**

| Callinectes sapidus | | | | | | | |
|---|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | | |
| Habitat conditions | 3 | | | | | | |
| Pressence status | + | | | | | | |
| Robustness | 3 | | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø | |

| | | | |
|---|---|---|---|
| = No | 1 = Low | - | = Not registered |
| = Low | 2 = Medimum | + | = Registered |
| = high | 3 = High | ++ | = Widely distributed |

## 3.7 Crassostrea gigas


### 3.7.1 Connectivity

The entire Kattegat, the Øresund and the Inner Danish Straits are identified as a highly connected area for *Crassostrea gigas* (Figure 13), consisting of 2 well-connected hydrographic regions (coherence values of 72 and 76 %) with a considerable bidirectional exchange of simulated agents between the two. Connectivity is limited towards the south east (at the boundary between Øresund and the wester Baltic Sea) due to larvae intolerance to brackish conditions. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) extends the hydrographic region of Kattegat and Øresund to include most of the Inner Danish Straits and the most western part of the Baltic Sea. Dispersal probability plots (Appendix 3) indicate that each of the major harbors Kattegat and Øresund (Copenhagen, Helsingør/Helsingborg, Grenå, Frederikshavn, Varberg and Gothenburg) are directly connected (i.e. within 1 generation) to several of the neighboring harbors and specifically across Kattegat.

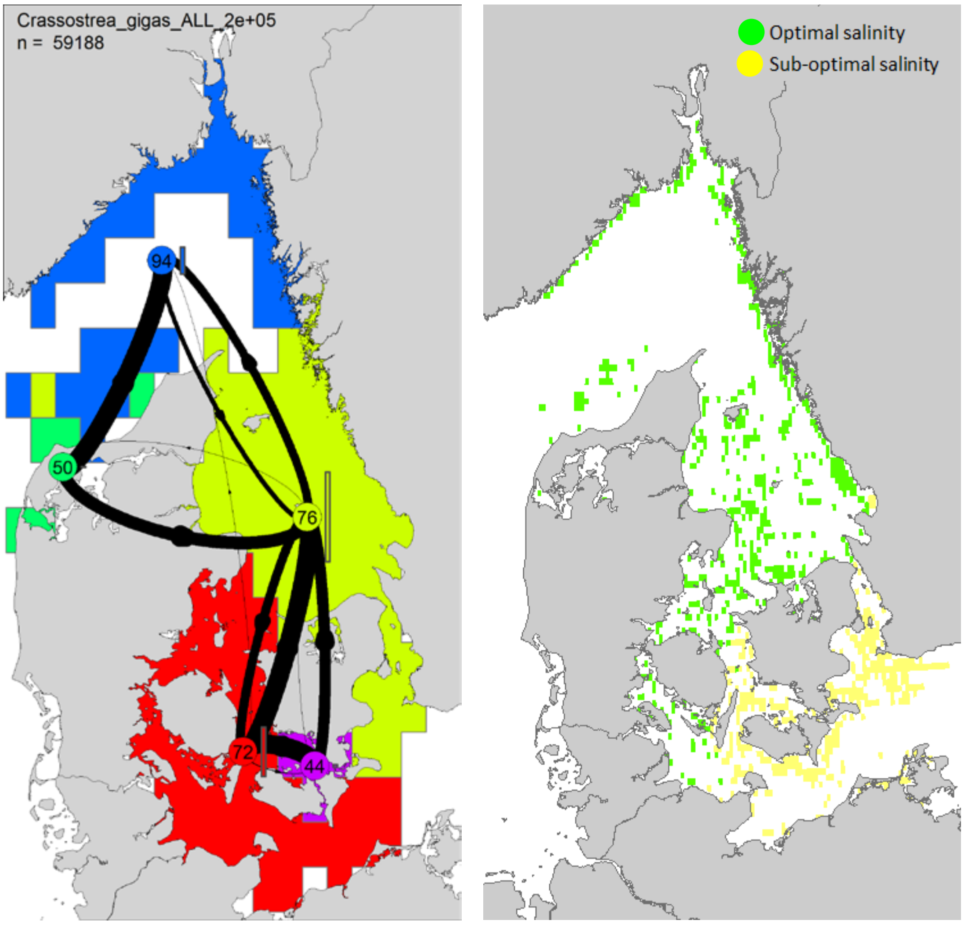



**Figure 13. Left: Hydrographic regions identified for *Crassostrea gigas* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix**

### 3.7.2 Robustness of results

In total 59 188 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Very similar results are found for individual years all identifying Kattegat and Øresund as one hydrographic region, or as 2 hydrographic regions with considerable bidirectional exchange of simulated agents between them. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows comparable result. Thus, the analysis results are considered robust.

### 3.7.3 Habitat characteristics

Habitats suitable for *C. gigas* in the larval dispersal simulation are highly fragmented and limited to hard substrate as defined in the EMODNET seabed habitat dataset. However, lavae of *C. gigas* are able to settle on other types of hard substrate including blue mussel beds, and established oyster beds (Dolmer et al. 2014). Larval settling in tidal and intertidal zones such as the Wadden Sea has also been recorded (Dolmer et al. 2014). Tidal flats or zones and existing mussels and oyster beds have not been included as habitats in the larval dispersal simulation. Thus, the physical habitat for *C. gigas* may not be adequately described. However, the number of agents included in the connectivity analysis and the robustness of the results indicate that the larval dispersal and habitat connectivities are sufficient to identify well-connected hydrographic regions. In Øresund the *C. gigas* may experience salinity condition below is salinity tolerance in shorter or longer periods.

### 3.7.4 Natural Dispersal potential

According to the Dolmer et al. (2014) *C. gigas* has been registered in Danish, Norwegian and Swedish waters, including the Wadden Sea and the Limfjord where commercial fisheries is ongoing. A massive invasion has been recorded in Scandinavia the previous decade. Although the species is widely registered in the Kattegat region, the species has not yet reached its maximum presence. *C. gigas* has a high reproductive potential producing 50-100 mill eggs per female. Temperature may be a limiting factor for reproduction since they need 4 to 8 weeks with more than 18°, and larva need approximately 225 temperature days to successfully settle (Anglès d'Auriac et al. 2017, Syvret et al. 2008).

### 3.7.5 Summary

Larvae of *C. gigas* are expected to disperse efficiently within the whole of Kattegat and Øresund. The species is registered throughout the region and although the species has not reached its maximum presence and distribution.

**Table 9. Connectivity ratings and species characteristics for *C. gigass*. For details on ratings descriptions see methodology section in this appendix.**

| Crassostrea gigas | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | ++ | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | |
|---|---|---|
| = No | 1 = Low | - = Not registered |
| = Low | 2 = Medimum | + = Registered |
| = high | 3 = High | ++ = Widely distributed |

## 3.8 Didemnum vexillum


### 3.8.1 Connectivity

Population connectivities of *Didemnum vexillum* (Figure 14) are highly limited by a short PLD (~1 day). Although suitable habitats are relatively small and fragmented, the habitat is evenly distributed throughout the Kattegat and the short PLD ensures that a relatively large fraction of simulated larvae successfully settle on neighboring habitat patches. The hydrographic regions are small and numerous with high within regions connectivities in Kattegat (82 – 100% coherence) indicating that connections across Kattegat in all direction are weak or not existing. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) show almost identical results. Dispersal probability maps indicate that none of the major harbors are directly connected via 1st generation dispersal. Dispersal probability maps of multiple generation dispersal (~ 5 years, 1 generation per year) indicate that theoretical connectivity may exist between the  all harbors in Kattegat (except ) although the probabilities are very small (< 0.1 %). Harbors of Copenhagen, Helsingør and Helsingborg are at the edge or outside of larval salinity tolerance limits.

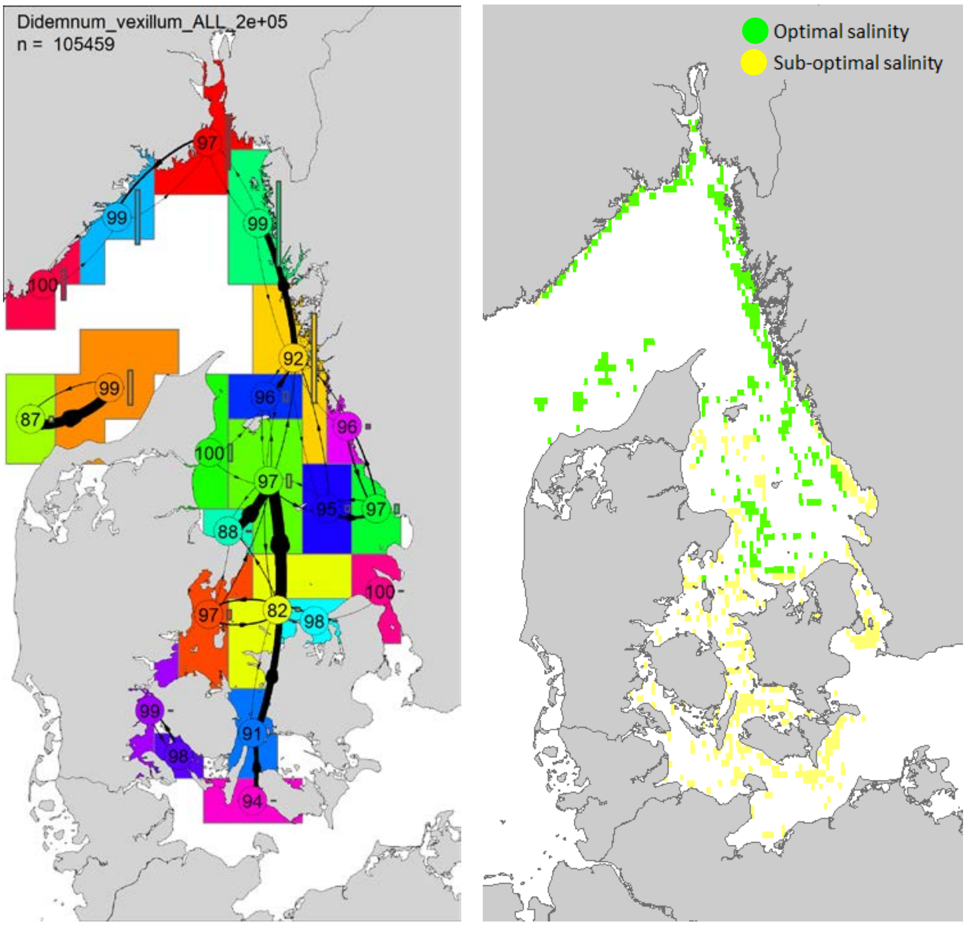



**Figure 14. Left: Hydrographic regions identified for *Didemnum vexillum* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.8.2 Robustness of results

In total 105 459 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Similar results are found for individual years with some deviation between years in the southward boundary of larval dispersal due salinity intolerance to low salinities, with the boundary location varying between the central Kattegat to the Inner Danish Straits. The sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows almost identical results. Thus, the analysis results are considered robust.

### 3.8.3 Habitat characteristics

Habitats suitable for *D. vexillum* in the larval dispersal simulation are fragmented and limited to hard substrate as defined in the EMODNET seabed habitat dataset and including water depth down to 65 meters. The spatial resol**u**tion of EMODNET seabed habitat maps is 250 meters. Smaller scale fragments of hard substrate habitats including artificial substrates (shoreline constructions and protection) and scattered stones and boulders in the littoral zone originating from quaternary moraine deposits are not resolved. According to Valentine et al. (2007), *D. vexillum* overgrows shellfish and other sessile invertebrate species, and gravel. Thus, the habitat map applied for the dispersal simulation may not include all suitable habitats. However, the relatively large number of simulated agents in the connectivity analysis, the relatively evenly distribution of fragmented habitats included, the very short PLD of 1 day, and finally the robustness of the hydrographic regions delineation indicate that a more adequately described habitat distribution and coverage will not have any major effect on the hydrographic delineation. In Øresund and in the shallow parts of central and southern Kattegat adult *D. vexillum* may experience salinity condition below the salinity tolerance in shorter or longer periods. Winter temperatures may be limiting for the extent of the population to deeper parts of Kattegat since populations have been reported to die at temperatures below 4$^{o}$C (Gitteberger 2007).

### 3.8.4 Natural Dispersal potential

According to the Strandberg (2017) *D. vexillum* has not yet been registered in Denmark, but is found in European waters of the Netherlands, Ireland and England (www.cabi.org). The larval dispersal is limited to 1 day or less. However, according to www.cabi.org some studies show evidence that detached fragments of *D.* vexillum (~tendrils) or colonies, colonies attached to shredded leaves or floating debris can reattach or relocate and disperse over long distances, and this type of rafting events may occur frequently, and thus may have a substantial effect on population dynamics. Thus, the simulated larval dispersal may not adequately represent the full natural dispersal potential.

### 3.8.5 Summary

The larvae of *D. vexillum* only exhibit very limited dispersal potential, and although habitats in Kattegat may be connected through multiple generation and stepping stone dispersal, it is unlikely that the species will disperse across the Kattegat due to larval transport. It is possible that rafts of tunic tendrils may disperse over larger distances; however, such dispersal is difficult to predict. Larval dispersal in Øresund is outside the salinity tolerance limit.

**Table 10. Connectivity ratings and species characteristics for *D. vexillum*. For details on ratings descriptions see methodology section in this appendix.**

| Didemnum vexillum | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 1 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | | |
|---|---|---|---|---|
| (red) = No | 1 | = Low | - | = Not registered |
| (yellow) = Low | 2 | = Medimum | + | = Registered |
| (green) = high | 3 | = High | ++ | = Widely distributed |

## 3.9 Ensis directus


### 3.9.1 Connectivity

In general, the connectivity patterns in Kattegat and Øresund are dominated by the relatively uneven distribution of suitable habitats. Dense coverage of habitats characterizes the shallow parts of western Kattegat, Øresund and the Inner Danish Straits, while habitats are scarce and fragmented along the Swedish west coast. The northern parts of Kattegat is divided into 2 hydrographic regions (Figure 15) with a high within regions connectivity (of 92 and 94 % coherence respectively). The exchange of simulated larvae across the Kattegat is primarily unidirectional with limited connectivity from west to east. The southern parts of Kattegat and Øresund are divided into 3 main hydrographic regions where the within regions connectivities are less strong (between 46 and 70 % coherence).

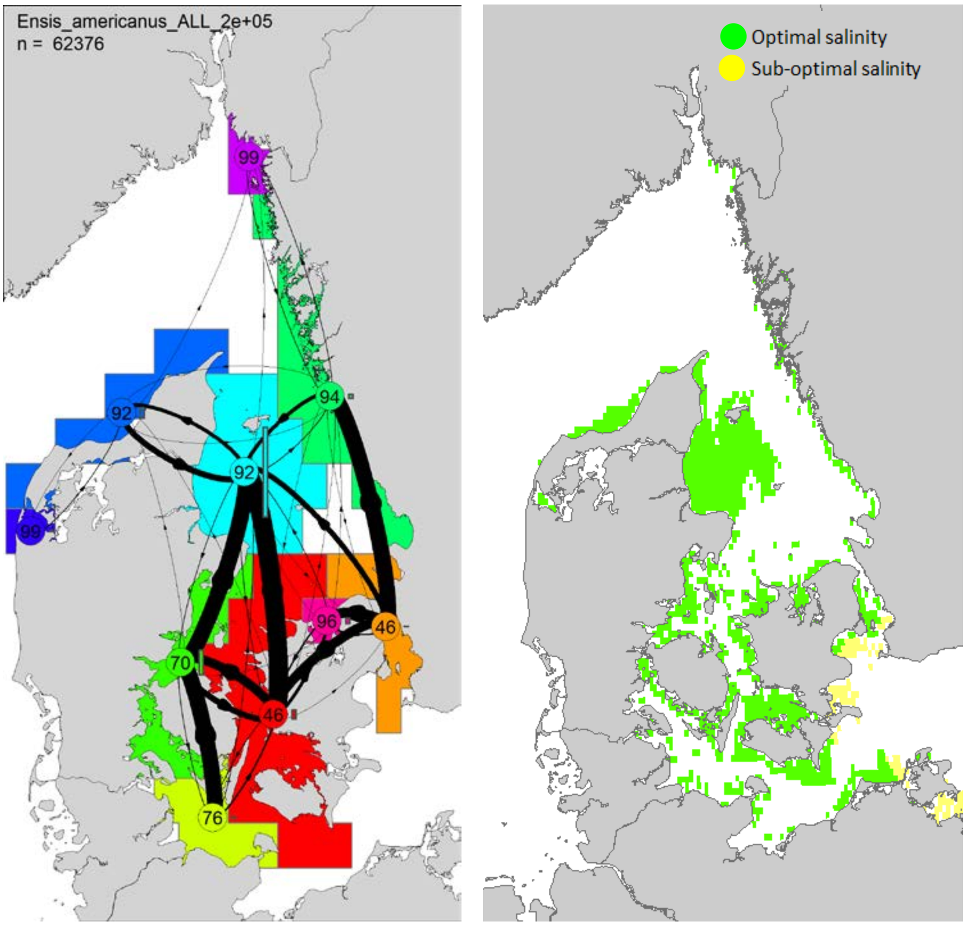



**Figure 15. Left: Hydrographic regions identified for *Ensis directus* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

While the connectivity in the south-north direction is strong, connectivity in the opposite direction exists but is limited. Sensitivity analysis carried out for 2005 restricting the larval dispersal depth between 0 m and 15 m (Appendix 3) show similar results. Dispersal probability plots (Appendix 3) indicate that in general the major harbors in the Kattegat (Grenå, Frederikshavn, Varberg and Gothenburg) are not directly connected (i.e. within 1 generation) across the Kattegat in both eastern and western directions. Multiple generation dispersal indicate that each harbor is connected to at least 2 other harbors (probabilities > 0.1 %) including bidirectional connectivity across the Kattegat. Øresund itself is well connected.

### 3.9.2 Robustness of results

In total 62 676 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. The results found for individual years (Appendix 3) vary considerably with deviations in the exact outline and size and extent of hydrographic regions. A consistent pattern in all 3 years however is the limited exchange of simulated agents across the Kattegat. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows relative robust results indicating that most of between years variability is caused by differences in hydrography between years. In contrast to the other marine invasive species included in species short list, E. directus spawning period is limited to the very early spring in March and April. The 3 hydrographic years included for the dispersal modelling are selected to reflect an average, and two diverging extremes of the winter North Atlantic Oscillation (NAO), which is expected to deviate most distinctly within the months of winter and early spring while deviations in summer months are expected to be vaguer. While the robustness of connectivity analysis results are considered robust, the variation between years must be considered.

### 3.9.3 Habitat characteristics

Habitats suitable for *E. directus* consist of relatively large contiguous areas of the shallow parts of western Kattegat, the Inner Danish Straits and the Øresund, while habitats along the west coast of Sweden are scarce and fragmented and may potential limit the connectivity across the Kattegat and along the Swedish west coast. Habitats are not expected to be limited by critical salinity or temperature conditions.

### 3.9.4 Natural Dispersal potential

The larvae of *E. directus* are limited to salinity levels above 15 PSU. The southward boundary representing the larval salinity intolerance varies considerably between the 3 years due to hydrographic conditions in the spawning season in early spring. In 2005 the southward boundary is located in the central Kattegat while in 2010 and 2012 are located at the entrance to the Baltic Sea. According to www.cabi.org, *E. directus* has a high reproductive potential and the ability to rapidly colonize new areas. The species was recorded the first time in Denmark in 1981 and since then registered at at least 40 locations between 2007 and 2015. Despite the distribution, the species is categorized as relatively rare (Miljøstyrelsen 2017).

### 3.9.5 Summary

The natural dispersal potential of *E. directus* is expected to cover the whole Kattegat and Øresund, however with limitation in dispersal across the Kattegat in both directions. The species is found relatively distributed however still considered rare.

**Table 11. Connectivity ratings and species characteristics for *E. directus*. For details on ratings descriptions see methodology section in this appendix.**

| Ensis americanus | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | ++ | | | | | |
| Robustness | 2 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | | | |
|---|---|---|---|---|---|
| (red) | = No | 1 | = Low | - | = Not registered |
| (yellow) | = Low | 2 | = Medimum | + | = Registered |
| (green) | = high | 3 | = High | ++ | = Widely distributed |

## 3.10 Eriocheir sinensis


### 3.10.1 Connectivity

The Kattegat is divided into 4 hydrographic regions separating eastern and western parts of Kattegat in both the south and the north (Figure 16) with some overlap with moderate to strong within regions connectivities (coherences of 69, 88, 88 and 90%) with some mutual exchange of simulated larvae between regions dominated by unidirectional linkages. In particular, the east to west dispersal in central and northern Kattegat is relatively weak. The results for individual years (2005, 2010 and 2012) identify most of the central and northern Kattegat as one well-connected region. This deviation from the lumped results for all years (Figure 14) indicate that this part of the region is connected however, the connectivity in the west and east directions are not conclusively strong. The southward boundary due to larvae intolerance to low salinities is located at the boundary between the Baltic Sea and the Inner Danish Straits and Øresund. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 m and 15 m (Appendix 3) shows similar results.

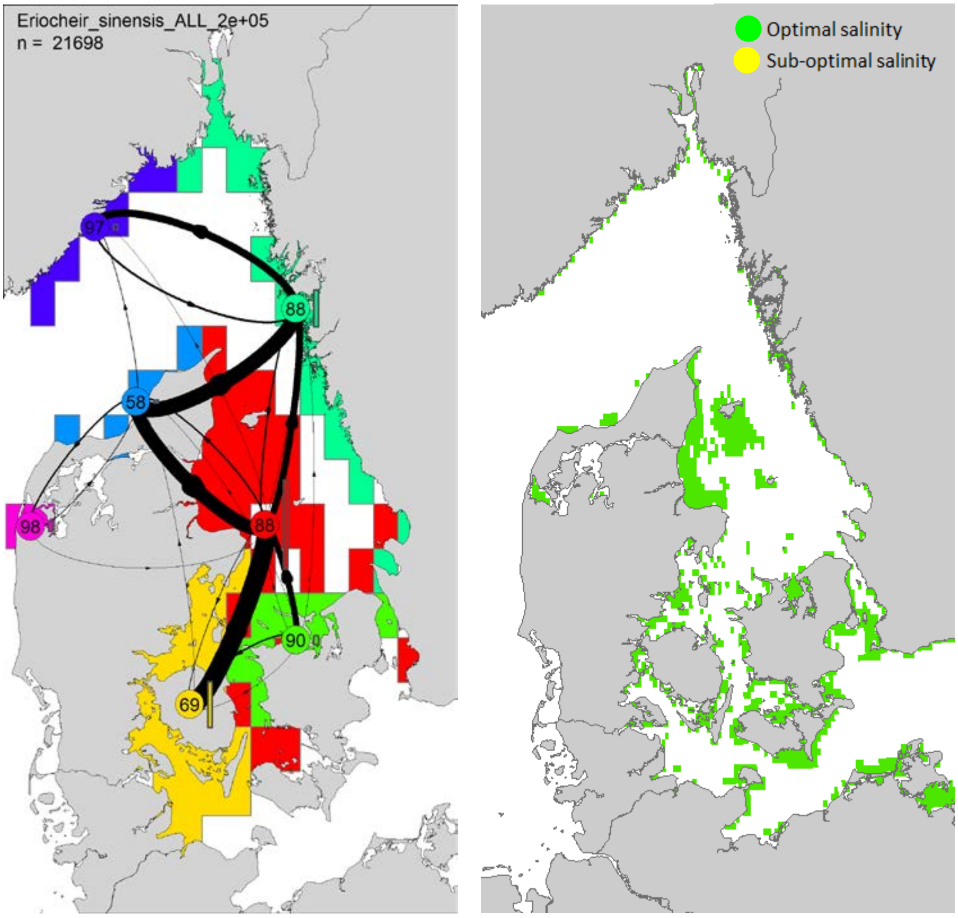



**Figure 16. Left: Hydrographic regions identified for *Eriocheir sinensis* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

Dispersal probability plots (Appendix 3) indicate that each of the 4 major harbors in the Kattegat (Grenå, Frederikshavn, Varberg and Gothenburg) are directly connected (i.e. within 1 generation) to at least one of the neighboring harbors and across Kattegat and along western and eastern shores. The harbors of Copenhagen, Helsingør and Helsingborg lie at or outside the larval salinity tolerance limits.

### 3.10.2 Robustness of results

In total 21 698 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Similar results are found for individual years with some variation in exact delineation and location of the southward boundary of larval dispersal due to intolerance to low salinity conditions, but overall supporting the same conclusion. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) show differences due to critical levels of agents used in the connectivity analysis for each year, however, the overall patterns support  the overall conclusion.  Thus, the analysis results are considered relative robust.

### 3.10.3 Habitat characteristics

Habitats are limited to shallow areas along the Danish coasts and parts of northwestern Kattegat, and only minor and fragmented areas along the west coast of Sweden. Although there is no limitation with respect to salinity and temperature intolerance levels for adult life stages according to www.cabi.org and the HELCOM/OSPAR target species list, Miljøstyrelsen (2017) suggests that temperature and salinity conditions may be limiting the development of larvae into adults in Danish waters.

### 3.10.4 Natural Dispersal potential

*E. sinensis* has a high reproductive potential females producing between 250,000 and 1 million eggs, PLD ranging from 30 to 60 days and the species is generally perceived as invasive (Miljøstyrelsen 2017) (www.cabi.org). The adult life stages can migrate over considerable distances and are tolerant to freshwater conditions. The species was registered for the first time in 1927, and is only found a few places in Danish waters.

### 3.10.5 Summary

Given the known tolerance limits of temperature and salinity for larvae and adults, the natural dispersal potential of *E. sinensis* is expected to cover the whole Kattegat due to a relatively good connectivity and very high reproductive potential. It has however been suggested that salinity and/or temperature is the main reason why the species only has been registered a few places despite an invasion history that goes back to 1927.

**Table 12. Connectivity ratings and species characteristics for *E. sinensis*. For details on ratings descriptions see methodology section in this appendix.**

| Eriocheir sinensis | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | + | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| Colour | | Rating | | Status | |
|---|---|---|---|---|---|
| Red | = No | 1 | = Low | - | = Not registered |
| Yellow | = Low | 2 | = Medimum | + | = Registered |
| Green | = high | 3 | = High | ++ | = Widely distributed |

## 3.11 Ficopomatus enigmaticus

*Source: www.europe-aliens.org (Dan Minchin)*

### 3.11.1 Connectivity

Most of Kattegat and Øresund is identified as a single well-connected hydrographic region ( ~ 80% coherence) delimited towards the south-east at the entrance to the Baltic Sea via Øresund, and to the south west towards a hydrographic region comprising the south western Kattegat and the Inner Danish Straits (Figure 17). To the north, the Kattegat region borders a region covering the Skagerrak. Mutual exchange of agents between the 3 regions exists, however dominated by unidirectional dispersal from south to north. The northward boundary is situated just north of Gothenburg. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) extends the central Kattegat hydrographic region towards the south to include the Inner Danish Straits. Dispersal probability plots (Appendix 3) indicate that each of the 7 major harbors in the Kattegat and Øresund (Grenå, Frederikshavn, Varberg, Gothenburg, Helsingør/Helsingborg, Copenhagen) are directly connected (i.e. within 1 generation) to at least one of the neighboring harbors including bidirectional connectivity across the Kattegat in east west directions. Connectivity is limited by scarce and fragmented habitat, which may be inadequately represented in the analysis, see below.

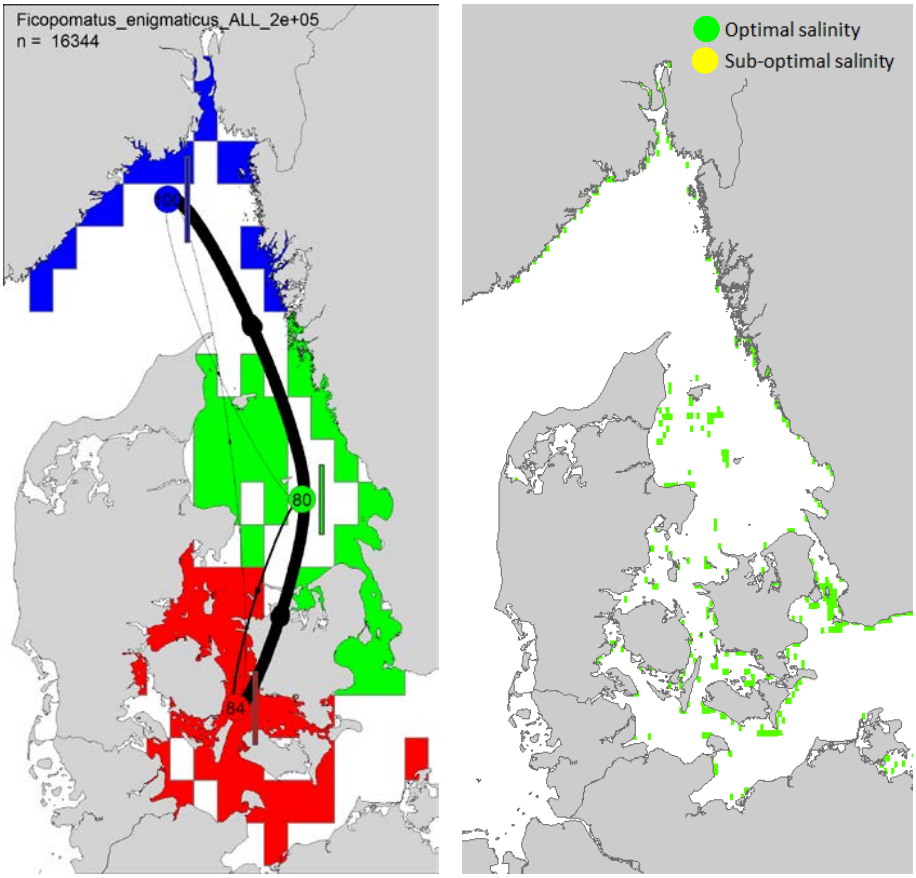



**Figure 17. Left: Hydrographic regions identified for *Ficopomatus enigmaticus based on 3 years larval dispersal simulation (2005, 2010 and 2012).* Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.11.2 Robustness of results

In total 16 344 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Results for individual years show very similar results with 2010 deviating from 2005 and 2012 by identifying the whole Kattegat and Øresund as one hydrographic region instead of two. However, results for all three years support the same conclusions. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows clear indications on critical levels of agents used in the connectivity analysis for each year when applying 50 000 agents.  Since results based on 200 000 agents per year show comparable results for all three years, the hydrographic regions delineation and extent are considered robust.

### 3.11.3 Habitat characteristics

Habitats suitable for *F. enigmaticus* are limited to hard substrates from the tidal zone down to 10 m. The spatial resolution of EMODNET seabed habitat maps is 250 meters. Smaller scale fragments of hard substrate habitats including artificial substrates (shoreline constructions and protection) and scattered stones and boulders in the littoral zone originating from quaternary moraine deposits are not resolved. *F. enigmaticus* is often found on concrete, stones and other hard substrates in harbors and shoreline constructions (DAISIE European Invasive Alien Species Gateway 2018). These are not included in the habitat map. Populations of *F. enigmaticus* in Denmark is found in Copenhagen harbor since 1997, and exists possibly in other locations as well (Miljøstyrelsen 2017), however the species expansion may be somewhat limited by water temperatures.

### 3.11.4 Natural Dispersal potential

Reported PLD of *F. enigmaticus* range between 20 and 25 days, and thus support relatively long dispersal distances. According to www.cabi.org larval survival vary considerable among habitats, and the ability of the species to further colonize habitats in Danish waters may be attributed to limitation due to larval intolerance to low temperatures. The limited succession of the species in Kattegat and Øresund despite its presence in Copenhagen harbor since 1997 indicates that environmental conditions supporting populations are limited.

### 3.11.5 Summary

Although the natural dispersal potential of *F. enigmaticus* is expected to cover the whole Kattegat and Øresund indications, suggest that the species may have some difficulties in expanding to other part of the region other than the Copenhagen harbor.

**Table 13. Connectivity ratings and species characteristics for *F. enigmaticus*. For details on ratings descriptions see methodology section in this appendix.**

| Ficopomatus enigmaticus | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | + | | | | | |
| Robustness | 2 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | |
|---|---|---|
| = No | 1 = Low | - = Not registered |
| = Low | 2 = Medimum | + = Registered |
| = high | 3 = High | ++ = Widely distributed |

## 3.12 Hemigrapsus sanguineus


### 3.12.1 Connectivity

The central and northwestern parts of Kattegat is identified as a relatively well-connected hydrographic region (~ 68% coherence) delimited towards the south and southeast due to larvae intolerance to brackish conditions (Figure 18). A boundary towards the north is located close to the transition zone between Kattegat and Skagerrak and stretching southwards along the west coast of Sweden to the south of Gothenburg. Connectivity towards the northeast is limited and predominantly unidirectional in the north and northeast direction. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) show more or less similar results with some deviation in the southward boundary due to larvae intolerance to low salinity. Dispersal probability plots (Appendix 3) indicate that the 3 major harbors in north and northeastern Kattegat (Frederikshavn, Gothenburg and Varberg) located inside the larval dispersal range are either directly connected via the 1st generation dispersal or via multiple generations dispersal. Dispersal from Gothenburg towards Frederikshavn and Varberg are weak. Dispersal from and to the harbor of Grenå is supported be very few successful agents due to critical salinity conditions. The harbors of Copenhagen, Helsingør and Helsingborg lie outside the larval salinity tolerance limits.

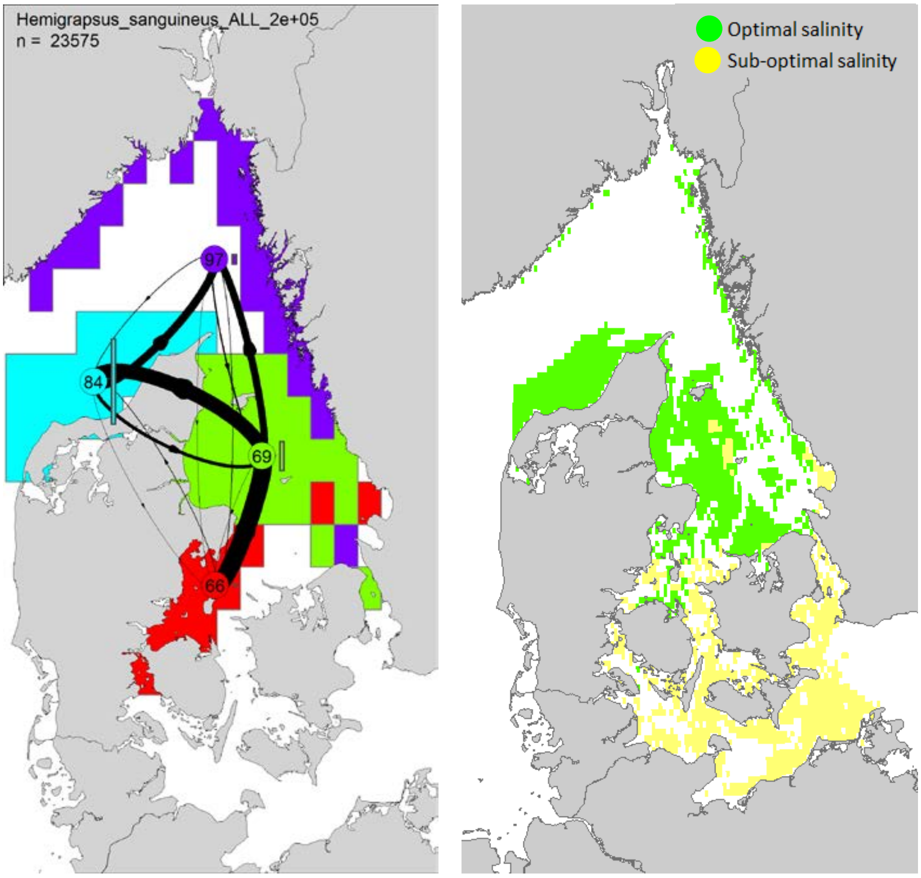



**Figure 18. Left: Hydrographic regions identified for *Hemigrapsus sanguineus* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.12.2 Robustness of results

In total 23 575 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Some variations in results are found for individual years, with especially 2005 supported by a critical number of agents originating from the Kattegat region included in the analysis. This can be explained by the larval salinity tolerance of 20 PSU in combination with a PLD of 16 days and the prevailing current directions resulting in a high chance of agents from Kattegat being transported through unfavorable salinity conditions. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows a more diffuse delineation of hydrographic regions due to a critical number of agents included in the analysis especially in the in the area close to the south-ward limitation in larval dispersal range due to intolerance to low salinity conditions. A simulation for 2010 using 1 000 000 agents (not presented) showed almost identical results compared to the simulation based on 200 000 agents. In conclusion the overall patterns of larval dispersal limited to the northern parts of Kattegat are relative robust, with year-to-year variations indicating that unsuccessful dispersal in the northern parts of Kattegat may occur.

### 3.12.3 Habitat characteristics

Habitats including sand and hard substrates down to 40 meters consist of large contiguous areas of the Kattegat and Øresund, except for the western part of Kattegat and along the west coast of Sweden where the habitats are more scarce and fragmented. While most of Kattegat lye well within the adult salinity tolerance, some shallow areas of central Kattegat and the most southern parts of Kattegat and the Øresund salinity conditions are below the salinity tolerance threshold for shorter or longer periods. According to Klassen (2012) *H. sanguine* can withstand salinities below 15 PSU for several hours and days, but viable populations are typically in areas with higher salinities. . Adult migration into more brackish waters is expected to be limited. Larvae are more sensitive to low salinity with at threshold of approximately 20 PSU, and is the expected to limit the extent of sustainable populations to the central and/or northern parts of Kattegat. No temperature in limitation is expected for larvae nor adult. The habitat conditions are considered suitable for reproducing population in the central and/or northern parts of Kattegat.

### 3.12.4 Natural Dispersal potential

*H*. *sanguine* female can produce up to 56 000 eggs producing larvae, 5-6 broods per year, and a PLD ranging from 16 to 55 days (inversely correlated to temperature) (Klassen 2012), and thus, the species is considered to have a high dispersal potential. In the current study we use the minimum value of reported PLD of 16 days while a PLD at water temperatures at 15 $^{o}$C of 55 days has been reported indicating that the connectivity calculated and presented here may be underestimated. The species presence has been recorded along the Atlantic coastline of Europe including the English canal and southern parts of the North Sea and recent years the species has been found on the west coast of Sweden (Jungblut et al. 2017). In Denmark recently, there have been unconfirmed single recordings of the species in 2018 in the several parts of Kattegat, the Inner Danish Straits and Øresund (Miljøstyrelsen, Danish Invasive species registration portal).

### 3.12.5 Summary

The natural dispersal potential of *H. sanguine* is expected to cover at least the central and northern parts of Kattegat. Current registrations (confirmed and unconfirmed) indicate that the species is present in Kattegat and the current distribution may reach as far as to the southern parts of Kattegat and the Øresund. The latter is however still subject to confirmation. Connectivity is expected to be high within the parts of Kattegat where salinity conditions are suitable for larval survival.

**Table 14. Connectivity ratings and species characteristics for *H. sanguineus*. For details on ratings descriptions see methodology section in this appendix.**

| Hemigrapsus sanguineus | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | + | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | |
|---|---|---|---|
| (red) = No | 1 = Low | - | = Not registered |
| (yellow) = Low | 2 = Medimum | + | = Registered |
| (green) = high | 3 = High | ++ | = Widely distributed |

## 3.13 Hemigrapsus takanoi


### 3.13.1 Connectivity

The larval connectivity is limited to the northern most parts of Kattegat due to larval intolerance to salinities below 25 PSU. Above this salinity a one hydrographic region is identified covering the northern parts of Kattegat and the southern and eastern parts of Skagerrak (Figure 19) indicating that connectivity is high with a within region connectivity of 85% and with a primarily unidirectional connectivity towards the part of Skagerrak. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) shows a similar result as for the year 2005 with a drift depth of 0 to 40meters, identifying the whole Kattegat and Skagerrak as a single hydrographic region. Dispersal probability plots (Appendix 3) indicate that for the two major harbors of northern Kattegat (Frederikshavn and Gothenburg) the dispersal probabilities for Gothenburg is limited by the number of agents included in the analysis indicating, that larval dispersal in northern Kattegat is close to the critical salinity conditions for larval stages. The harbors of Grenå, Varberg, Copenhagen, Helsingør and Helsingborg all lie outside the larval salinity tolerance limits .

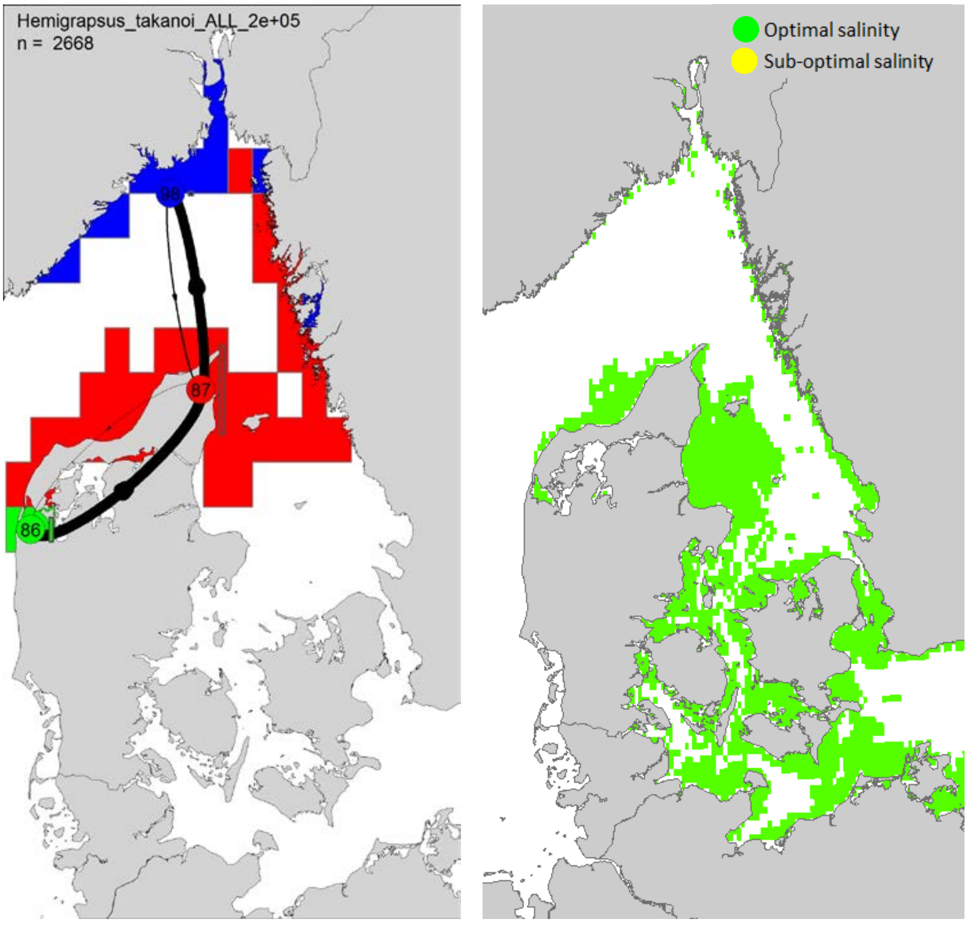



**Figure 19. Left: Hydrographic regions identified for Hemigras tankoi based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.13.2 Robustness of results

In total 2 668 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. This at a very critical number of agents and is due a combination of low larval salinity tolerance and a high PLD of 30 days increasing the likelihood of simulated larvae experiencing critical salinity conditions during drift, and a conveyance of the remaining simulated agent towards the North Sea.  Results from individual years show similar patterns, however, identifying northern Kattegat and Skagerrak as one hydrographic region. Although the number of simulated agents is very critical, the location of the southward boundaries of the hydrographic region is consistent. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows a more diffuse delineation of hydrographic regions. This is due to the critical number of agents included in the analysis .The exact delineation of hydrographic regions in northern Kattegat is not robust, however, the southwards extent of the region reflecting larval salinity tolerance is considered robust. Connectivity across the northern Kattegat is uncertain, and may despite the long PLD, be limited by larval salinity tolerance during drift.

### 3.13.3 Habitat characteristics

Habitats include all types of habitats down to 20 meters and consist of large contiguous areas of the Kattegat and Øresund all areas lying well within the adult salinity tolerance. The potential colonization of the habitat will be limited by the larval intolerance to water salinity below 25 PSU, and the ability of post-larval life stages to migrate from larval settling sites in the north via southward migration into the central and southern parts of Kattegat, the Inner Danish Straits and the Øresund. Because *H. takanoi* is a relative newly identified species, it is uncertain if water temperature may be a limiting factor for the colonization ability of *H. takanoi* in the Kattegat and Øresund region.

### 3.13.4 Natural Dispersal potential

Although knowledge on the reproductive potential of *H. takanoi* is limited, females are expected to produce more than 50 000 eggs, and have several broods a year, and combined with a PLD up to 30 days depending water temperature (www.cabi.org) the species is considered to have a high dispersal potential. Brink et al. (2013) found successful ovary development in females collected in Dutch waters at temperatures above 15ºC and larval development duration decreasing from 86 days at 12 ºC to 28 days 18 ºC. In the current study, we use the minimum value of reported PLD of 30 days, while a PLD; however, shorter PLDs may occur in warmer waters. The species has been found in  Denmark in 2018 in the Inner Danish Straits at two locations (Miljøstyrelsen, Danish Invasive species registration portal) which indicate that despite the limitation in larval connectivity expected due to intolerance to salinities below 25 PSU, the species is able to migrate long distances and potential inhabit all parts of Kattegat and Øresund.

### 3.13.5 Summary

The natural dispersal potential of *H. takanoi* is presumably high but expected to cover primarily the northern parts of Kattegat. Current registrations (confirmed) that the species is present in the Inner Danish Straits indicate that adult migration may be considerable and within the entire Kattegat and Øresund region. It is however questionable if this can lead to high abundances in areas south of the most northern parts of Kattegat.

**Table 15. Connectivity ratings and species characteristics for *H. takanoi*. For details on ratings descriptions see methodology section in this appendix.**

| Hemigrapsus takanoi | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 1 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | + | | | | | |
| Robustness | 1 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| Colour | | Rating | | Status | |
|---|---|---|---|---|---|
| Red | = No | 1 | = Low | - | = Not registered |
| Yellow | = Low | 2 | = Medimum | + | = Registered |
| Green | = high | 3 | = High | ++ | = Widely distributed |

## 3.14 Hydroides dianthus

### 3.14.1 Connectivity

The larval connectivity is limited to the northern most parts of Kattegat and the Skagerrak due to larval intolerance to salinities below 25 PSU dividing the area into 3 hydrographic regions (Figure 20). The northern Kattegat is included in one hydrographic region with a coherence of 73 % and a distinct and predominantly unidirectional connectivity to toward the Skagerrak. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) shows almost identical results as for dispersal depth between 0 and 40 meters. The year 2005 deviates from 2010 and 2012 with a southward boundary located further north due to larval intolerance to critical salinity conditions. Dispersal probability plots (Appendix 3) is limited by the number of agents included in the analysis for the northern parts of Kattegat, however indicating that for the two major harbors of northern Kattegat (Frederikshavn and Gothenburg) there is a direct (1 generation) but unidirectional (~eastwards) connectivity between the two harbors. Multiple generation dispersal probabilities show that harbors are likely to be connected in both directions during a 5-year period, however with a clear bias towards an east-west transfer of simulated larvae.

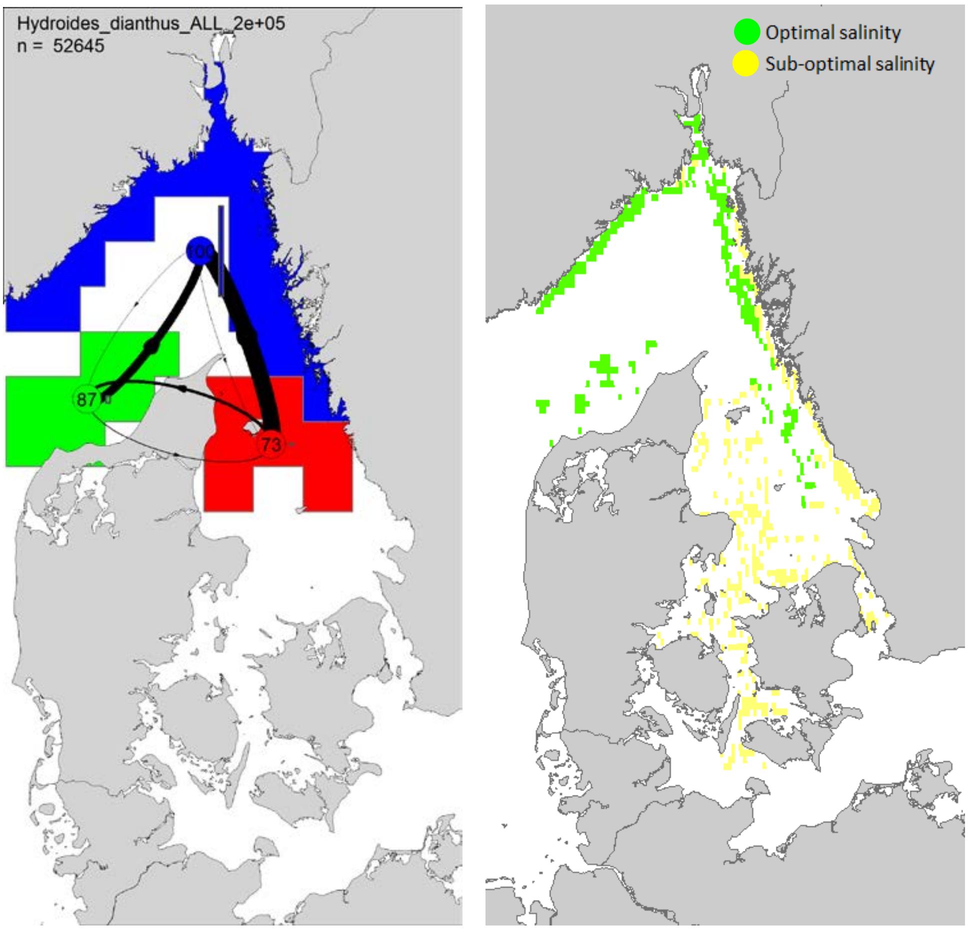



**Figure 20. Left: Hydrographic regions identified for *Hydroides dianthus* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.14.2 Robustness of results

In total 52 645 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. The single largest proportion of agents included in the connectivity analysis originates from spawning sites in the Skagerrak. Only a small number of agents support the delineation of the hydrographic region of northern Kattegat. Results from individual years show very similar patterns in 2010 and 2012. In 2005, the northern Kattegat is more or less excluded from the connectivity analysis indicating that year-to-year differences in hydrographic dynamics may expose larvae to various degrees of unfavorable salinity conditions. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) show similar patterns, with the extent and delineation of the northern parts of Kattegat being limited by the number of agents originating in Kattegat included in the connectivity analysis. The results are considered relative robust, however, the connectivity across the northern Kattegat is expected to be sensitive to year-to-year differences in hydrographic conditions.

### 3.14.3 Habitat characteristics

Habitats include hard substrate down to 200 meters and consist of fragmented but regularly distributed areas of the Kattegat and Øresund. The habitat coverage may be somewhat underestimated since hard surfaces of on-shore constructions such as harbors and shoreline protections, and patches less than the resolution of the EMODNET habitat data of250 meters are not included. In addition, hard surfaces associated with stones and cobble in the littoral zone originating from quaternary moraine deposits are not included. Most of the habitats in Kattegat and Øresund are exposed to sub-optimal conditions of salinity for adult *H. dianthus* during shorter and longer periods, with local optimal condition extending southwards following the deeper parts of the eastern Kattegat. The potential colonization of the habitat will also be limited by the larval intolerance to water salinity below 25 PSU. From previous invasion histories covering both temperate and tropic regions, temperature is not expected to be a limitation for adult life stages.

### 3.14.4 Natural Dispersal potential

According to Lenone (1970), *H. dianthus* female produces up to 30 000 mature ova and reaches maturity in 12-25 days. Toonen and Pawlik (2001) refer to maturation time between 17-31 days. The combination of large reproductive output, multiple generations within a season and PLD between 5 and 14 days indicate a high dispersal potential if conditions are optimal. Optimal salinity conditions however seems to be limited to the northern parts of Kattegat. *H. dianthus* has not been registered in Danish or Swedish waters.

### 3.14.5 Summary

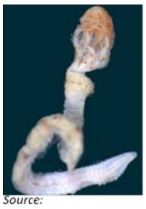
Although the natural dispersal potential of *H. dianthus* is high adult and larvae intolerance to low salinities is expected to be a major limitation to the distribution of the species in most of Kattegat and Øresund. The most northern parts of Kattegat is included within the larval dispersal range, however a very low number of simulated agents supports this and therefor here considered as outside the expected larval dispersal range.

**Table 16. Connectivity ratings and species characteristics for *H. dianthus*. For details on ratings descriptions see methodology section in this appendix.**

| Hydroides dianthus | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | |
|---|---|---|
| Red = No | 1 = Low | - = Not registered |
| Yellow = Low | 2 = Medimum | + = Registered |
| Green = high | 3 = High | ++ = Widely distributed |

## 3.15 Laonome calida



Source:
www.australianmuseum.net.au
(© Grontmij | team Ecologie)

### 3.15.1 Connectivity

Population connectivities of *Laonome calida* are highly limited by a short PLD (~1 day). Very little information is found on this species and some uncertainty exist on the taxonomic classification and if the recordings of the species are in fact representing different species (Capa et al. 2014). Due to the lack of information of this species, preferred habitat is assumed to include all substrate types down to 40 m depth with no limitation due to adult or larval salinity tolerances. Connectivity results based on these assumptions identify a number of small regions in Kattegat and the Øresund (Figure 21) with coherence values between 76 – 94 % indicating that connections across Kattegat in all direction are weak. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) shows almost identical results. Dispersal probability maps indicate that none of the major harbors in Kattegat are directly connected via 1st generation dispersal. Dispersal probability maps of multiple generation dispersal indicate that theoretical connectivity may exist between the all harbors in Kattegat but the probabilities are small (< 0.1 %). Harbors of Copenhagen, Helsingør and Helsingborg are well connected.

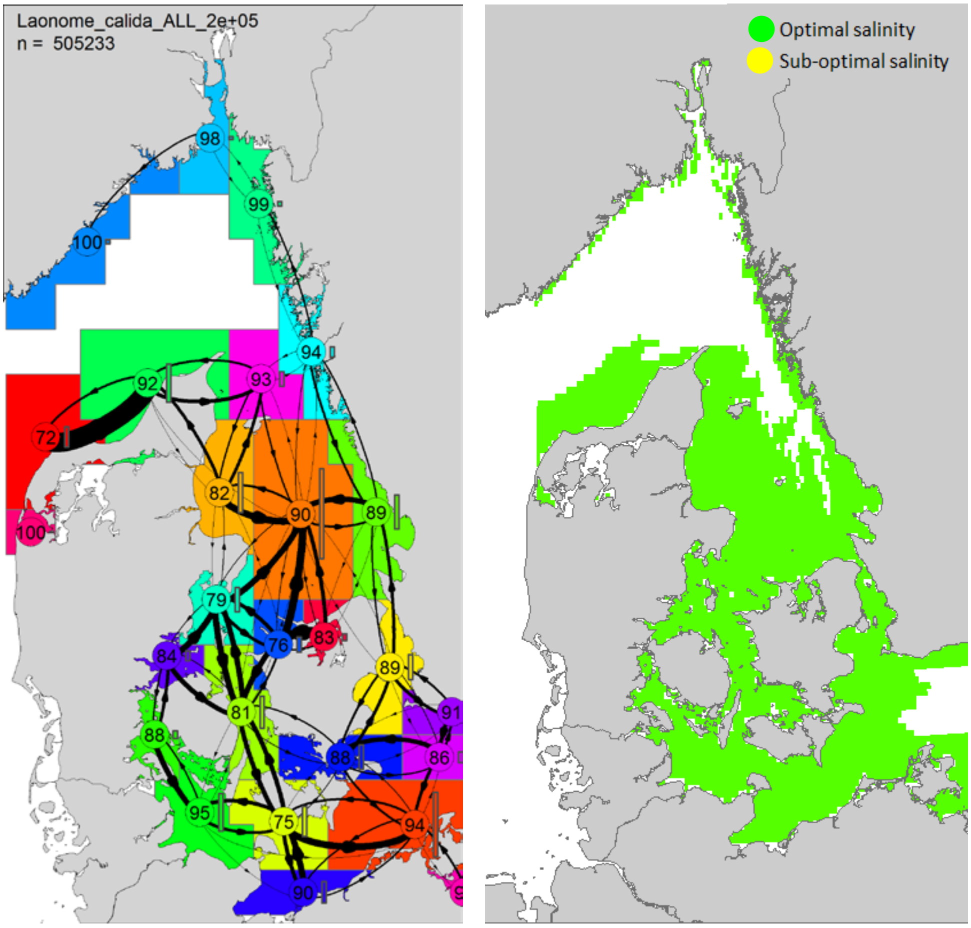



**Figure 21. Left: Hydrographic regions identified for *Laonome calida* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.15.2 Robustness of results

In total 505 233 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Almost identical results are found for individual years. Thus, the analysis results given the assumptions applied are considered robust.

### 3.15.3 Habitat characteristics

Very little information exists on the habitat requirements. The specimens has been reported from open water marine environments while specimens found in Netherlands were exclusively associated with tidal and non-tidal estuarine and even freshwater conditions (Capa et al. 2014). Recently the species has been reported from the Estonian part of the Baltic Sea (Brik et al. 2018). No reports have been found of the species occurring in high salinity conditions outside its assumed native occurrences in Australia. Habitat conditions found in The Netherlands comprise a large variety of substrate types (Capa et al. 2014). Given the uncertainty of habitat preference, environmental tolerances and taxonomy, the representativeness of the habitat applied in the connectivity analysis is low and very uncertain.

### 3.15.4 Natural Dispersal potential

The natural dispersal potential is limited by the short PLD of approximately 1 day. Registrations in The Netherlands and Estonia indicate that the species is able to disperse efficiently locally, but with little dispersal potential over larger distances. The lack of marine registrations outside its presumed native region may indicate that the population found in European waters have limited tolerance to marine salinity levels; however, this is speculative.

### 3.15.5 Summary

Due to the short PLD the connectivity is limited. In case that both habitat conditions and environmental conditions are less optimal than conditions assumed in the connectivity analysis, the limitation in connectivity will be even more pronounced. Only the Øresund is identified as well connected.  Salinity intolerance however is unknown.

**Table 17. Connectivity ratings and species characteristics for *L. calida*. For details on ratings descriptions see methodology section in this appendix.**

| Laonome calida | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | |
| Habitat conditions | 1 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | | | |
|---|---|---|---|---|---|
| (red) | = No | 1 | = Low | - | = Not registered |
| (yellow) | = Low | 2 | = Medimum | + | = Registered |
| (green) | = high | 3 | = High | ++ | = Widely distributed |

## 3.16 Marenzelleria viridis


### 3.16.1 Connectivity

The Kattegat and the Inner Danish Straits are identified as belonging to one hydrographic region (Figure 22) with a high within region connectivity (coherence of 98 %). Some noise in the hydrographic region delineation towards the north is due to the vicinity to the upper salinity threshold for larval tolerance. The entire region is highly connected due to a combination of a long PLD of 28 days, a relative extensive habitats coverages and extreme tolerance to high and low salinity conditions. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) extents the hydrographic region of Kattegat to include the eastern and northern parts of Skagerrak. Dispersal probability plots (Appendix 3) indicate that each of all the major harbors of Kattegat and Øresund (except Frederikshavn) are directly connected (i.e. within 1 generation) to two or more of the neighboring harbors including bidirectional connection across the Kattegat.

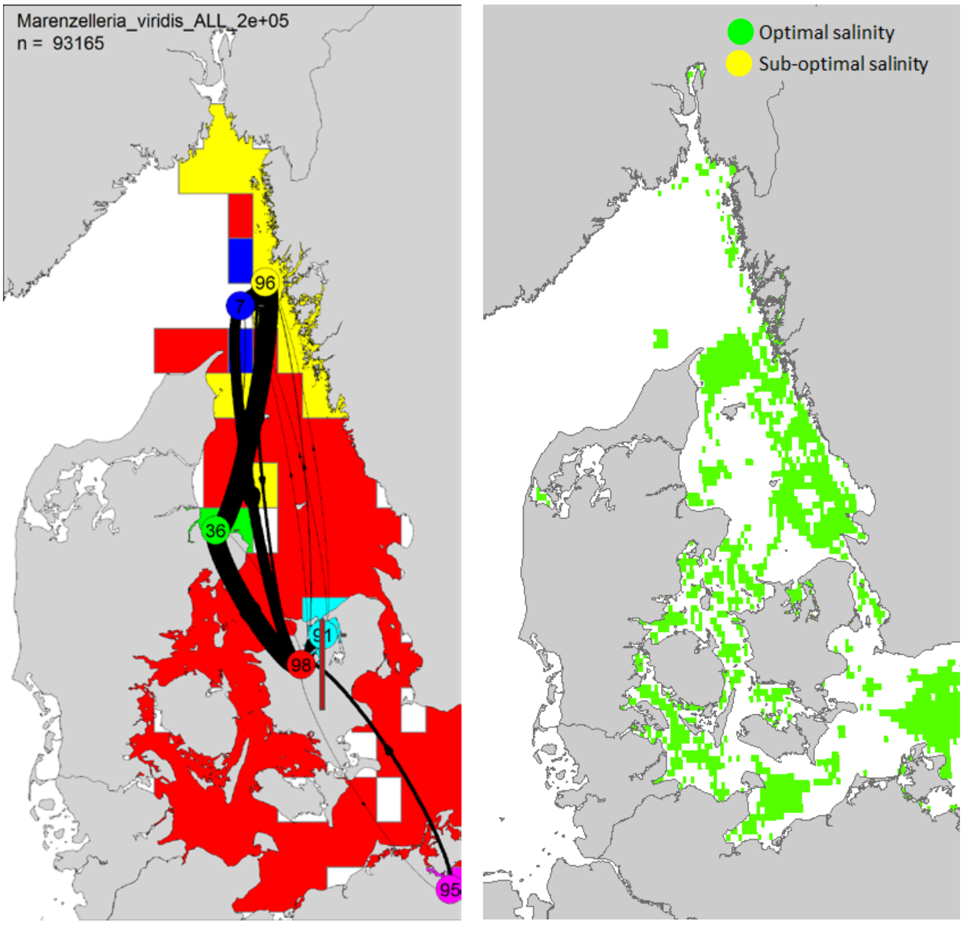



**Figure 22. Left: Hydrographic regions identified for *Marenzelleria viridis based on 3 years larval dispersal simulation (2005, 2010 and 2012).* Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.16.2 Robustness of results

In total 93 165 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Results from individual years show similar patterns with 2005 dividing the Kattegat and Øresund into 2 separate regions with bi-directional exchange of agents. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) supports this conclusion where most of the area in all years belongs to one major hydrographic region. Although the delineation of hydrographic regions in the Kattegat using 50 000 agents is somewhat more diffuse due to the location of Kattegat close to the upper salinity threshold for larval salinity tolerance. The results supporting a conclusion of a highly connected area are considered robust.

### 3.16.3 Habitat characteristics

Habitats include muddy substrate down to 65 meters and covers relatively large and contiguous areas in particular in the deeper parts of the study area.  The whole of Kattegat and Øresund is exposed to optimal conditions of salinity for adult *M. viridis.* Larval intolerance to salinities above 30 PSU limits the northwards potential distribution in the Skagerrak however is not expected to limit dispersal in Kattegat.

### 3.16.4 Natural Dispersal potential

Bochard (1997) found the number of eggs per female between 10 000 and 46 000 eggs and compared with the long PLD between 28 and 49 days the dispersal potential is high. According to Kristensen et al. (2012) *M. viridis* are found throughout the Kattegat and Øresund region and can be considered as widely distributed in Danish waters.  Newly published data found that the genus *Marenzelleria* dominating many of the deeper parts of the Baltic consists of three species: *M. viridis, M. arctia and M.* nectlecta (Kauppi et al. 2018). It is not known to what extent these three species may be present in Kattegat and Øresund and it is unclear how life history traits may differ between species.

### 3.16.5 Summary

The Kattegat and Øresund region is well connected and the dispersal potential of the *M. viridis* is supported by the widespread occurrences registered throughout the region. It is possible that the taxonomy of the species in the region is not fully resolved.

**Table 18. Connectivity ratings and species characteristics for *M. viridis*. For details on ratings descriptions see methodology section in this appendix.**

| | Marenzelleria viridis | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | ++ | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| Colour | | Rating | | Status | |
|---|---|---|---|---|---|
| red | = No | 1 | = Low | - | = Not registered |
| yellow | = Low | 2 | = Medimum | + | = Registered |
| green | = high | 3 | = High | ++ | = Widely distributed |

## 3.17 Mytilopsis leucophaeata

Source: www.nobanis.org)

### 3.17.1 Connectivity

The central Kattegat is divided into a western and a eastern region (Figure 23) with high within region connectivity (coherence of 97 and 100 %) and with no or very limited uni-directional exchange of simulated larvae from west to east. Further south the hydrographic regions have an intermediate within regions connectivity (coherences of 58-91 %) and with a considerable bi-directional exchange of simulated agent. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) show very similar results. Dispersal probability plots (Appendix 3) indicate that the harbors of Øresund (Helsingborg/Helsingør and Copenhagen) are well connected via 1st generation dispersal whereas no direct connectivity exists between the major harbors of Kattegat (Grenå, Frederikshavn, Varberg and Gothenburg). Multiple generation dispersal probability maps show that most of the region connected, however in Kattegat probabilities are very small (< 0.1 %) and mostly theoretical.

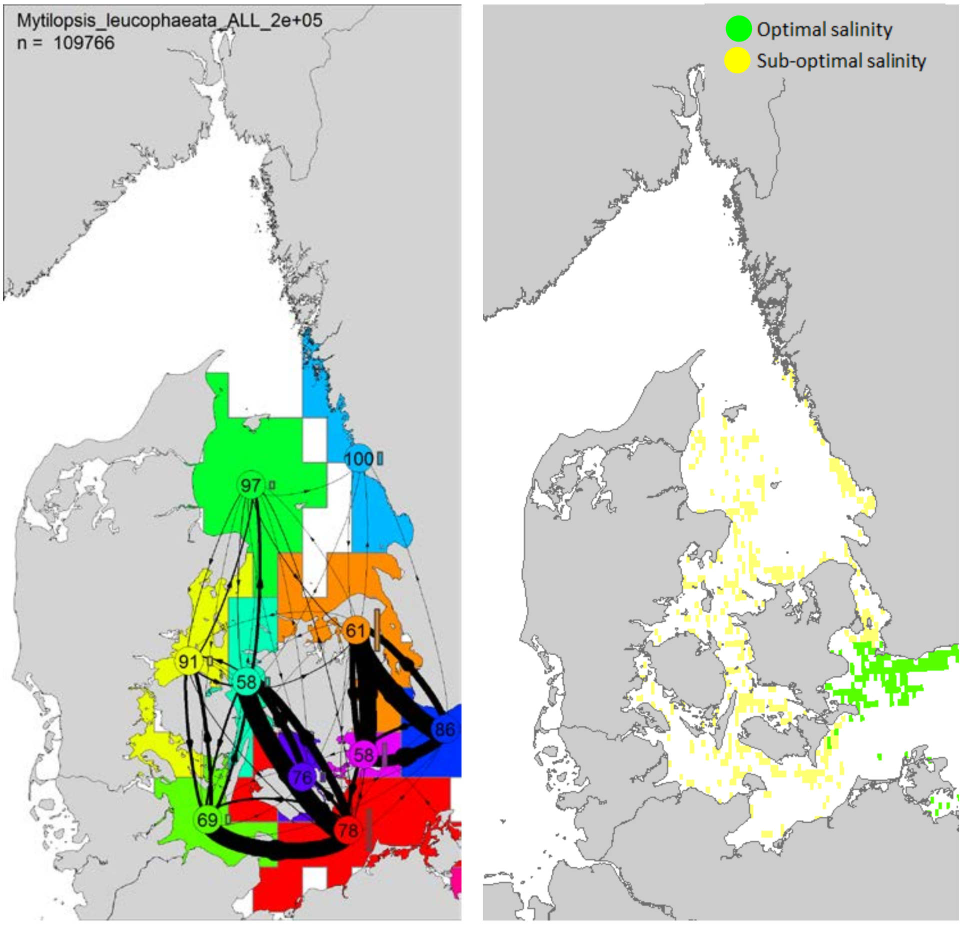



**Figure 23. Left: Hydrographic regions identified for *Mytilopsis leucophaeata based on 3 years larval dispersal simulation (2005, 2010 and 2012).* Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.17.2 Robustness of results

In total 109 766 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. While most of the delineated southern hydrographic regions of the Inner Danish Straits, Øresund and the Wester Baltic Sea are based on relatively large number of simulated agents, the hydrographic regions of Kattegat are based on limited number of agents. This is due to the simulated larval intolerance to salinity conditions above 25 PSU, which also is responsible for the northward boundary of the extent of larval dispersal located at the transition zone between Kattegat and Skagerrak. Results from individual years show very similar patterns supporting the same conclusions. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) again show similar results. Thus, the results are considered robust.

### 3.17.3 Habitat characteristics

Habitats include hard substrate down to assumable 40 meters comprising fragmented habitats with limited coverage. The spatial resolution of EMODNET seabed habitat maps is 250 meters. Smaller scale fragments of hard substrate habitats including artificial substrates (shoreline constructions and protection) and scattered stones and boulders in the littoral zone originating from quaternary moraine deposits are not resolved. Different information sources on salinity tolerance of *M. leucophaeata* are inconsistent. E.g. according to Verween et al. (2006) and the Swedish factsheet (www.frammandearter.se) the species is described as a brackish water species with tolerance interval between 0.5 and 18 PSU, while the European Network on Invasive Alien Species (www.nobanis.org) refers to laboratory experiments documenting that the species survive from <1ppt to “full strength” of seawater. Invasion histories however suggest that the species is mostly found in brackish water less than 10 ppt. Larval development is unaffected by salinities 10 and 32 ppt (at 26$^{o}$C), but some studies find that reproduction is triggered by a decrease in salinity. Thus, it is unclear to which extent the species can establish in Kattegat and Øresund region apart from at location of freshwater outlet, however, the dispersal of larvae is expected not to be limited. It is uncertain if winter temperatures may be a limiting factor the ability of the species to establish viable populations.

### 3.17.4 Natural Dispersal potential

According to www.nobanis.org *M. leucophaeata* reproduce throughout the season from spring to early autumn, and is characterized as having a high reproductive potential. In the current study we use the minimum value of reported PLD of 6 days while the maximum reported PLD is 14 days. Thus, the connectivity calculated presented here may be under estimated. *M. leucophaeata* has been recorded in Europe since 1835 (www.nobanis.org) and since then along the coasts of the North Sea and the Baltic Sea. Especially in relation to river outlets and as fouling agents on cooling water systems.

### 3.17.5 Summary

The Øresund is well connected, while the connection in Kattegat is limited to the western and eastern parts of Kattegat respectively with no connectivity across Kattegat. Although the larval dispersal presumably is insensitive to the salinity conditions in Kattegat and Øresund it is questionable to what extent the species may establish in Kattegat and Øresund apart from coastal areas affected by freshwater output.

**Table 19. Connectivity ratings and species characteristics for *M. leucophaeata*. For details on ratings descriptions see methodology section in this appendix.**

| Mytilopsis leucophaeata | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ (red) | N (red) | S (green) | W (yellow) | E (red) | Ø (green) |

| | | |
|---|---|---|
| (red) = No | 1 = Low | - = Not registered |
| (yellow) = Low | 2 = Medimum | + = Registered |
| (green) = high | 3 = High | ++ = Widely distributed |

# 3.18 Mytilus galloprovincialis


## 3.18.1 Connectivity

The central and northern parts of Kattegat and the Øresund are identified as belonging to 1 hydrographic region (Figure 24) with a strong within region connectivity (coherence 88 %). A bi-directional exchange of simulated larvae connects this region to the the southwestern Kattegat, the Inner Danish Straits and the wester Baltic Sea. A boundary to the north is located at the transition zone between the Kattegat and the Skagerrak, with limited bi-directional exchange of simulated agents. Sensitivity analysis carried out for 2005 restricting the larval dispersal depth to between 0 m and 15 m (Appendix 3), show very similar results. Dispersal probability plots (Appendix 3) indicate that each of the 7 major harbors in the Kattegat and Øresund (Grenå, Frederikshavn, Varberg, Gothenburg, Copenhagen, Helsingør/Helsingborg) are directly connected (i.e. within 1 generation) to at least one of the neighboring harbors. Connectivity across Kattegat is strong in the east-west direction, while connectivity in the opposite direction in particular from the harbor of Gothenburg may require more than 1 generation.

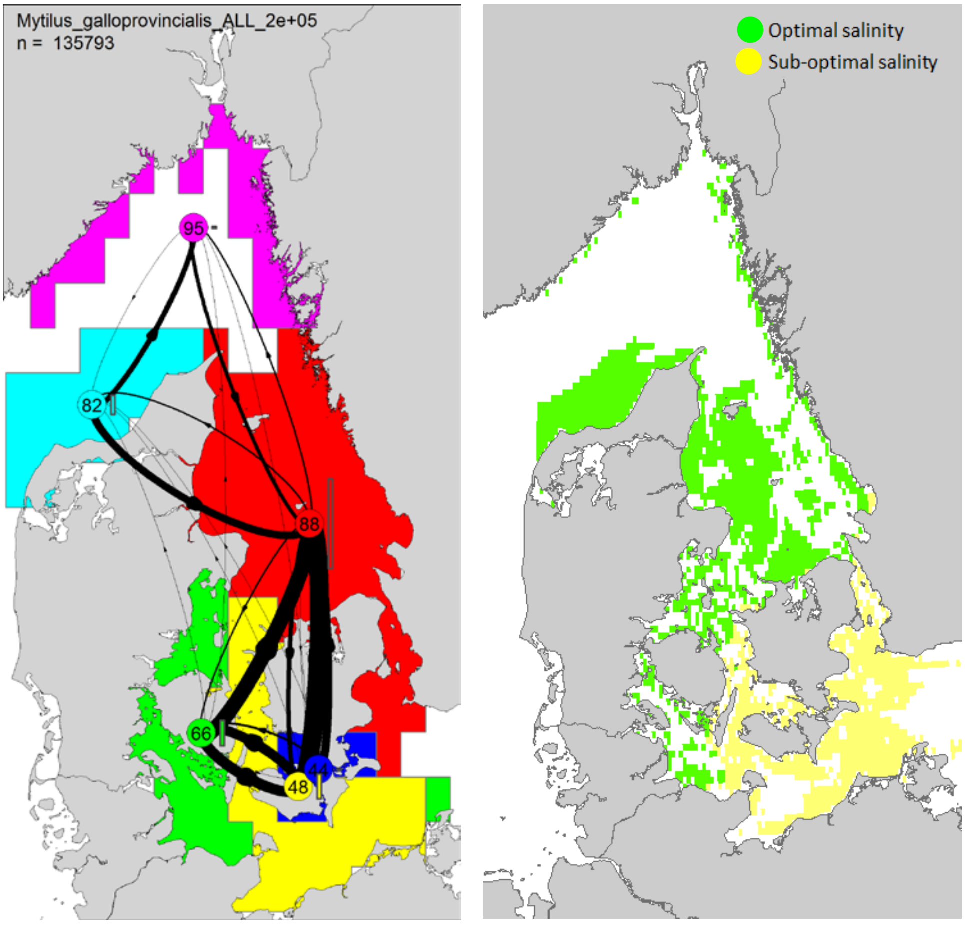



**Figure 24. Left: Hydrographic regions identified for *Mytilus galloprovincialis based on 3 years larval dispersal simulation (2005, 2010 and 2012).* Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.18.2 Robustness of results

In total 135 793 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Almost identical results are found for individual years with 2010 identifying the whole Kattegat and Øresund as belonging to 1 hydrographic region. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows very similar results. The analysis results are considered robust.

### 3.18.3 Habitat characteristics

Habitats include sand and hard substrate down to 40 meters comprising contiguous habitats with large coverage. While salinity conditions in Kattegat are expected to be optimal, *M. galloprovincialis* may experience sub-optimal salinity conditions for adult life stages in Øresund during shorter or longer periods.

### 3.18.4 Natural Dispersal potential

*M. galloprovincialis* has a high reproductive potential. Females produce 1.5 – 3.5 million eggs, may reproduce throughout the season from spring to early autumn, and the species may multiple generations per years Fofonoff et al. (2018). In the current study we use the minimum value of reported PLD of 14 days while the maximum reported PLD is 28 days. Thus, the connectivity calculated presented here may be underestimated. According to the World Register of Marine Species (MolluscaBase 2018), *M. galloprovincialis* has been recorded in Europe in the North Sea area including Belgium, Holland, Ireland and the United Kingdom. But in recent years the species and *M. galloprovincialis/M. edulis* hybrids have been observed along the Norwegian coast (Brooks and Farmen 2013), and lately Mathiesen et al. (2017) found the presence of *M. galloprovincialis* or their hybrids in SW Greenland.  The presence and distribution of *M. galloprovincialis* in Denmark or Sweden is unknown.

### 3.18.5 Summary

The natural dispersal potential of *M. galloprovincialis* is large and Kattegat and Øresund are expected to be highly interconnected and to support viable populations of *M. galloprovincialis* and hybrids.

**Table 20. Connectivity ratings and species characteristics for *M. galloprovincialis*. For details on ratings descriptions see methodology section in this appendix.**

| Mytilus galloprovincialis | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | |
|---|---|---|
| (red) = No | 1 = Low | - = Not registered |
| (yellow) = Low | 2 = Medimum | + = Registered |
| (green) = high | 3 = High | ++ = Widely distributed |

## 3.19 Palaemon macrodactylus


Source: Torres et al. 2012. Medit. Mar. Sci., 13/2, 2012, 278-282

### 3.19.1 Connectivity

The whole of Kattegat, the Øresund, the Inner Danish Straits and the western Baltic Sea are identified as belonging to one hydrographic region (Figure 25) with a strong within region connectivity (coherence of 100 %). This is primary due to the relative high PLD of 15 days, short generation time potential supporting multiple generations per season and large and contiguous habitats with no limitation regarding larval or adult salinity tolerances. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) show similar results supporting the same conclusions. Dispersal probability plots (Appendix 3) indicate that each of the 7 major harbors in the Kattegat and Øresund (Grenå, Frederikshavn, Varberg, Gothenburg, Copenhagen, Helsingør/Helsingborg) are directly connected (i.e. within 1 generation) to at least two or more of the neighboring harbors and in particular across the Kattegat bi-directional in the east-west direction.

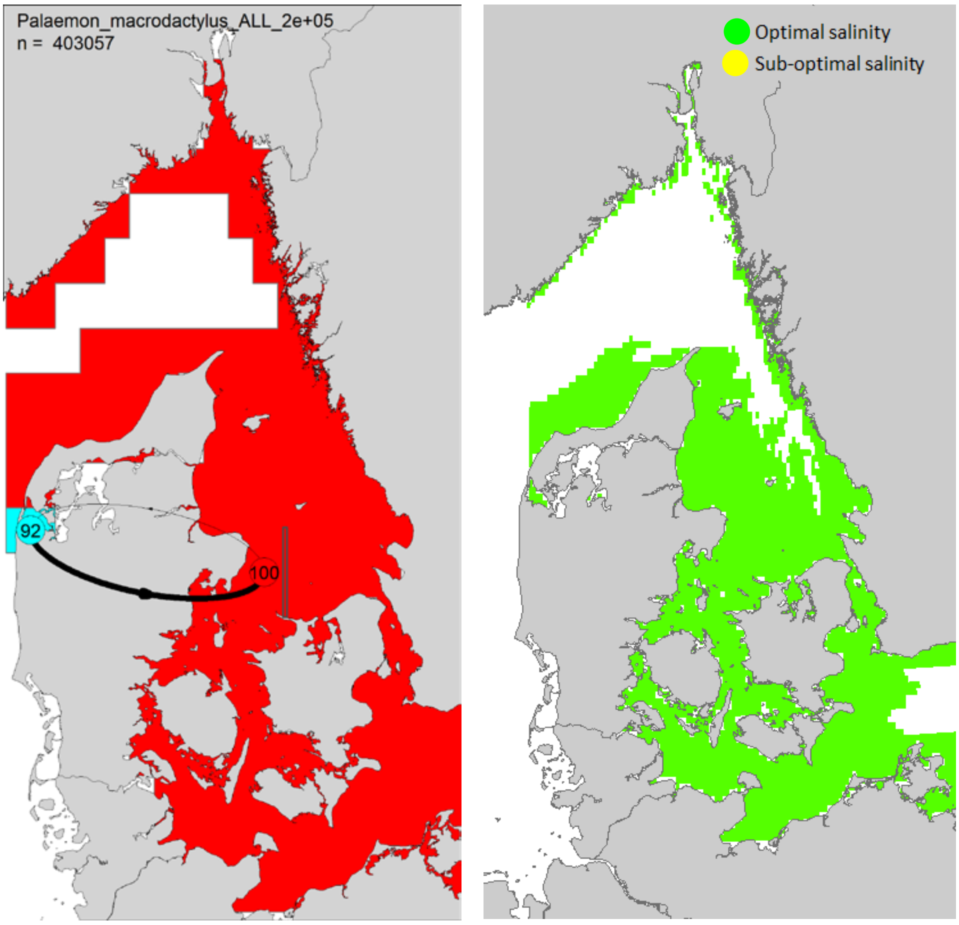



**Figure 25. Left: Hydrographic regions identified for *Palaemon macrodactylus* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

## 3.19.2 Robustness of results

In total 403 057 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Almost identical results are found for individual years identifying the whole of Kattegat and Øresund belonging to a single well-connected area. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) shows very similar results. The analysis results are considered robust.

## 3.19.3 Habitat characteristics

Habitats include all types of substrate down to 40 meters, and thus almost the entire seabed of Kattegat and Øresund except for the deepest parts of eastern and northern Kattegat. Salinity conditions are expected to be optimal for both adult and larvae of *P. macrodactylus*. No studies were found suggesting that temperature can be expected to be a limiting factor.

## 3.19.4 Natural Dispersal potential

According to CABI (www.cabi.org), *P. macrodactylus* has a high reproductive potential. Females produce 500 – 2800 larvae with multiple broods per year, reproduction occurs throughout the season from spring to early autumn, and the species may have multiple generations per years. According to the CABI *P. macrodactylus* has been recorded in Europe in the North Sea area including Belgium, Holland, Germany and the United Kingdom, and in the Baltic Sea in Poland and Germany. The presence and distribution of *P. macrodactylus* in Denmark or Sweden has not been recorded, although it is plausible the species is already present.

## 3.19.5 Summary

The natural dispersal potential of *P. macrodactylus* is large, and the Kattegat and Øresund are expected to be highly interconnected. The area is expected to support viable populations of *P. macrodactylus*.

**Table 21. Connectivity ratings and species characteristics for *P. macrodactulys*. For details on ratings descriptions see methodology section in this appendix.**

| Palaemon macrodactylus | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | | | |
|---|---|---|---|---|---|
| (red) | = No | 1 | = Low | - | = Not registered |
| (yellow) | = Low | 2 | = Medimum | + | = Registered |
| (green) | = high | 3 | = High | ++ | = Widely distributed |

## 3.20 Potamocorbula amurensis

Source: www.cabi.org (U.S. Geological Survey, CA.)

### 3.20.1 Connectivity

The western and central parts of Kattegat are identified as belonging to 1 hydrographic region (Figure 26) with a strong within region connectivity (coherence of 93 %). The west coast of Sweden is identified as a separate hydrographic region similarly with a strong within region connectivity (coherence of 96 %). Connectivity across the Kattegat is limited however bi-directional. To the south, the Kattegat hydrographic regions border three major hydrographic regions via weak but bi-directional exchange of simulated larvae. These include southwestern and southern parts of Kattegat and the Øresund all extending into the Inner Danish Straits and/or the Baltic Sea. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) identifies the whole of Kattegat area (except the south-west corner and Øresund) as a single hydrographic region indicating the near surface dispersal increase the cross-Kattegat connectivity. Dispersal probability plots (Appendix 3) indicate that each of 5 of the 7 major harbors in Kattegat and Øresund (Grenå, Varberg, Copenhagen, Helsingør/Helsingborg) are directly connected (i.e. within 1 generation) to at least one of the neighboring harbors. The connectivity between harbors of Gothenburg and Varberg towards Frederikshavn and Grenå require multiple generation and even so the dispersal probabilities are very low (< 0.1 %).

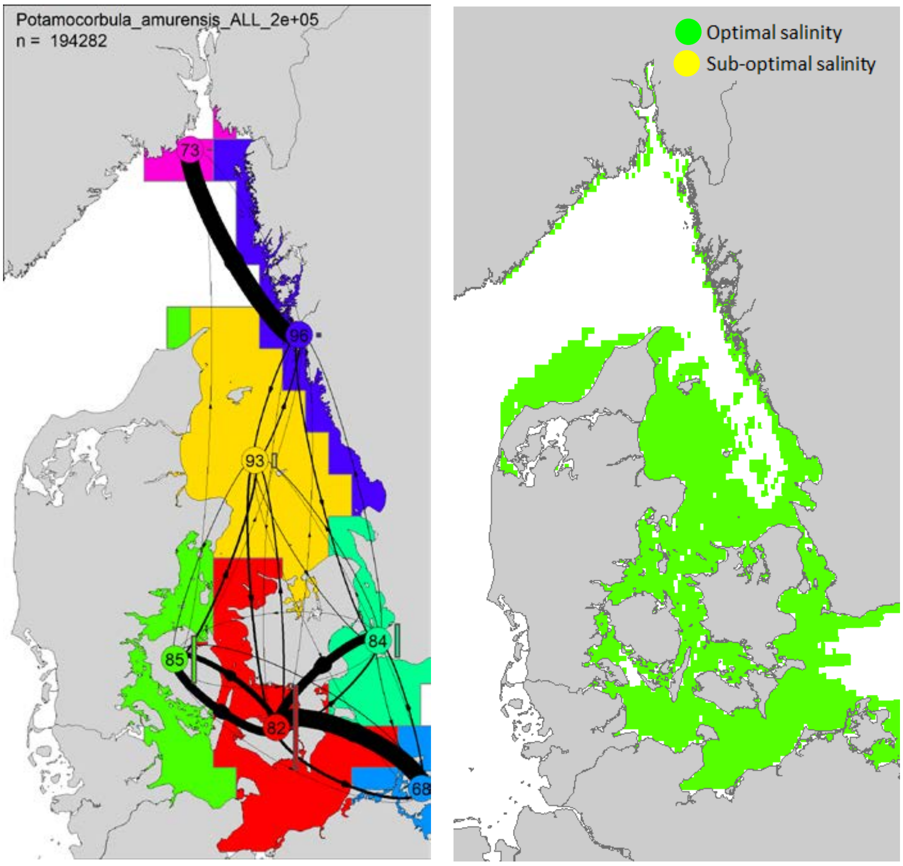




**Figure 26. Left: Hydrographic regions identified for *Potamocorbula amurensis* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

## 3.20.2 Robustness of results

In total 194 282 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Almost identical results are found for individual years. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) likewise shows similar results with a slightly more diffuse patterns in the hydrographic regions delineation in the Kattegat region due to critical number of agents. The analysis results using 200 000 agents are considered robust.

## 3.20.3 Habitat characteristics

Habitats include all types of substrate down to 30 meters, and thus cover almost the entire seabed of Kattegat and Øresund except for the deepest parts of eastern and northern Kattegat. Salinity conditions are expected to be optimal for both adult and larvae of *P. amurensis*. Temperature is not expected to be a limiting factor.

## 3.20.4 Natural Dispersal potential

According to CABI (www.cabi.org), *P. amurensis* has a high reproductive potential. Females produce 45,000-220,000 oocytes including at least two broods per year, reproduction occurs throughout the season from spring to early autumn and the species may support multiple generation per years. In the current study, we use a PLD of 14 days, while the reported PLDs range between 14-21 days. A longer PLD may increase the cross Kattegat connectivities. No studies were found documenting *P. macrodactylus* in Denmark or Sweden.

## 3.20.5 Summary

The natural dispersal potential of *P. amurensis* is large, and the Kattegat and Øresund are expected to be interconnected with some limitation however in the east- west direction from especially the Swedish harbors of Varberg and Gothenburg to the Danish harbors of Frederikshavn and Grenå. The Kattegat and Øresund area is expected to support viable populations of *P. macrodactylus* and hybrids.

**Table 22. Connectivity ratings and species characteristics for *P. macrodactylus*. For details on ratings descriptions see methodology section in this appendix.**

| Potamocorbula amurensis | | | | | | | |
|---|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | | |
| Habitat conditions | 3 | | | | | | |
| Pressence status | - | | | | | | |
| Robustness | 3 | | | | | | |
| Connectivity: | | KØ | N | S | W | E | Ø |

| Colour | | Rating | | Status | |
|---|---|---|---|---|---|
| Red | = No | 1 | = Low | - | = Not registered |
| Yellow | = Low | 2 | = Medimum | + | = Registered |
| Green | = high | 3 | = High | ++ | = Widely distributed |

## 3.21 Rangia cuneate

Source:
www.nonnativespecies.org

### 3.21.1 Connectivity

A number of hydrographic regions is found in the southern parts of Kattegat, the Øresund, the Inner Danish Straits and the western Baltic Sea, all with variable within regions connectivities (coherences between 54-100%) (Figure 27). Two shallow areas of central and southeastern Kattegat are identified as isolated hydrographic regions (coherences of 100 %), but based on a very low number of agents. The rest of Kattegat lies outside the larval salinity tolerance range. No or very little connectivity is found between hydrographic regions of the southern Kattegat and the Øresund, primary due to these regions being located at the edge of the salinity tolerance range for the larval stage. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) shows almost identical results. Dispersal probability plots (Appendix 3) indicate that the 3 major harbors in Øresund (Copenhagen, Helsingør/Helsingborg) are directly connected (i.e. within 1 generation) while the remaining harbors are outside the larval salinity tolerance range

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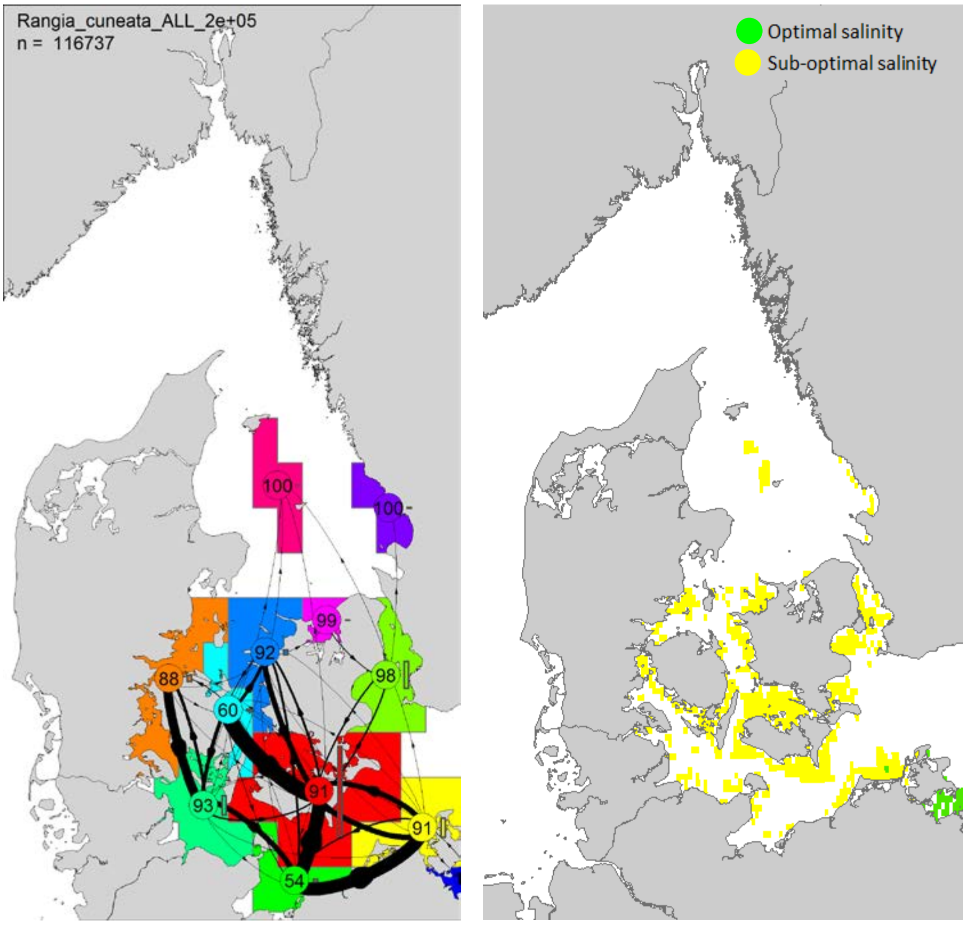


**Figure 27. Left: Hydrographic regions identified for *Rangia cuneate* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.21.2 Robustness of results

In total 116 737 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Almost identical results are found for individual years. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) likewise show almost identical results. Thus, the results are considered robust.

### 3.21.3 Habitat characteristics

Habitats include sand and muddy substrates down to 15 meters, and thus comprise the shallow and coastal areas of Kattegat and Øresund. Populations of *R. cuneate* are typically found in brackish water with salinities between 1 and 15 PSU (www.nonnativespecies.org), however, Cooper (1981) reported that adult *R. cuneate* is capable of adapting to salinities from 0 – 33 ppt. Larval salinity tolerances according to Cain (1973) is between 2 and 20 PSU, with an optimal range between 2 and 10 PSU. With some uncertainty on the exact salinity tolerance reported for adults, the salinity range where *R. cuneate* is typically found, suggests that salinity conditions are expected to be sub-optimal for R. *cuneate* in the entire Kattegat and Øresund region during shorter or longer periods. It is uncertain to which extent the species is able to establish in the region apart from coastal areas exposed to freshwater runoff.  Temperature is not expected to be a limiting factor.

### 3.21.4 Natural Dispersal potential

According to (www.nonnativespecies.org) *R.* cuneate has shown to be highly invasive if the conditions are right where the species within only a few years has come to dominate the bivalve faunas. It was first recorded in European waters in 2005 in Belgium (Verween et al. 2006) and later in Poland (Warzocha et al. 2015) and Estonia (Möller and Kotta 2017) where populations continue to spread. The presence and distribution of *R. cuneate* in Denmark or Sweden has not been recorded.

### 3.21.5 Summary

The natural dispersal potential of *R. cuneate* has shown to be very effective locally once introduce and if conditions are optimal. While the central and northern parts of Kattegat lye outside salinity tolerance of the species, sub-optimal conditions exists in the southern parts of Kattegat and the Øresund. In these parts no or very limited connectivity exists. It is uncertain to which extent the species is able to establish in this part of the region apart from coastal areas exposed to freshwater runoff.

**Table 23. Connectivity ratings and species characteristics *R. cuneate.* For details on ratings descriptions see methodology section in this appendix.**

| Rangia cuneata | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 1 | | | | | |
| Habitat conditions | 1 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| Colour | Rating | | Status | |
|---|---|---|---|---|
| Red = No | 1 | = Low | - | = Not registered |
| Yellow = Low | 2 | = Medimum | + | = Registered |
| Green = high | 3 | = High | ++ | = Widely distributed |

## 3.22 Rapana venosa


### 3.22.1 Connectivity

The central and eastern parts of Kattegat and the Øresund belong to 1 hydrographic region, while the remaining parts of Kattegat is divided into 3-4 hydrographic regions (Figure 28). Common for all hydrographic regions is a relatively low to intermediate within connectivity (coherences between 32 – 90%) and with considerable bi-directional exchange of simulated larvae indicating that the entire area is well connected. Only exception is the most southwestern parts of Kattegat where the simulated larval exchange is dominantly uni-directional towards the north. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) identify the Kattegat and Øresund as 1 well connected region except for most southwestern corner. Dispersal probability plots (Appendix 3) indicate the 6 of the major harbors of Kattegat and Øresund (Grenå, Frederikshavn, Varberg, Gothenburg and Helsingør/Helsingborg) are directly connected (i.e. within 1 generation) to at least one of the other harbors. Some connections between harbors may require more than 1 generation. Copenhagen harbor is located close to the southward extension of larval dispersal due to larval intolerance to brackish conditions.

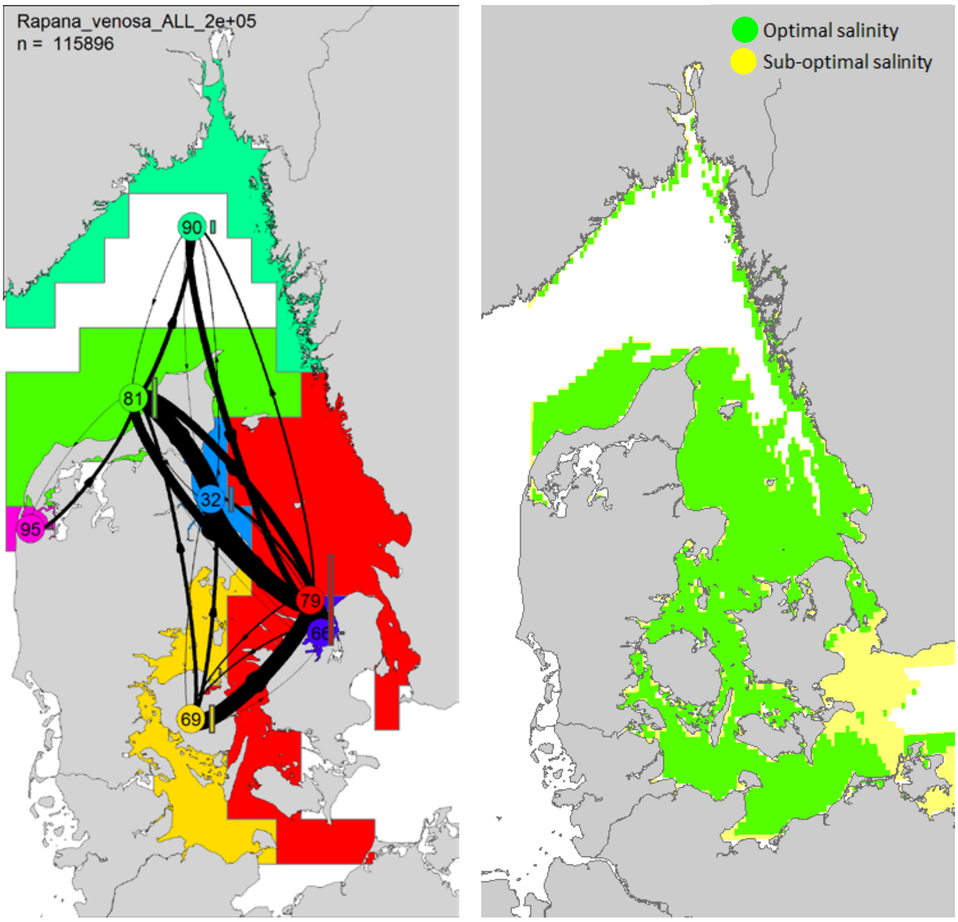


**Figure 28. Left: Hydrographic regions identified for *Rapana venosa* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.22.2 Robustness of results

In total 115 896 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Very similar results are found for individual years. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) likewise show very similar results. The results are considered robust.

### 3.22.3 Habitat characteristics

The preferred habitat include all types of substrates down to 40 meters and covers the entire Kattegat and Øresund except from the deepest parts of northern and eastern Kattegat. Salinity conditions for adult *R. venosa* are expected to be optimal for the entire Kattegat and Øresund. Reported temperature tolerance ranges from 4°C to 27°C (Global Invasive Species Database 2018). It is possible that the potential extent of this species in the Kattegat and Øresund will be dependent on migration to the deeper parts during cold winters and locations affected by cooling water outlet. Wu (1988) cited in ICES (2004) is referring to the ability of *R. venosa* to exploit estuarine regions with warm summer temperatures but possible surface freezing in winter via winter migration into deeper water.

### 3.22.4 Natural Dispersal potential

According to CABI (www.cabi.org), *R. venosa* is considered as one of the worst invaders worldwide. Females produce between 179 000 to 400 000 eggs and have a PLD of 14 days *(*Chung et al. 2002) with the ability to prolong the PLD up to 80 days (ICES 2004). Thus, the connectivity calculated and presented here may be underestimated. The species has been recorded multiple places in Europe (www.cabi.org ) with the UK, Belgium and the Netherlands. In 1992, the species was found on Dogger-bank in the North Sea (Miljøstyrelsen 2017). No records from the Kattegat and Øresund region have been found.

### 3.22.5 Summary

The natural dispersal potential of *R. venosa* is potential large, and connectivity analysis indicate that the Kattegat and Øresund region is well connected. The ability of species to colonize Kattegat and Øresund is questionable however due to intolerance to cold temperatures below 4 $^{o}$C, and it may depend on the ability of the species migrate to deeper and warmer water during the coldest season and the ability to maintain populations locally in areas affected by cooling water.

**Table 24. Connectivity ratings and species characteristics for *R. venosa*. For details on ratings descriptions see methodology section in this appendix.**

| Rapana venosa | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 3 | | | | | |
| Habitat conditions | 3 | | | | | |
| Pressence status | - | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | | |
|---|---|---|---|---|
| (red) = No | 1 | = Low | - | = Not registered |
| (yellow) = Low | 2 | = Medimum | + | = Registered |
| (green) = high | 3 | = High | ++ | = Widely distributed |

## 3.23 Rhithropanopeus harrisii

Source: www.cabi.org (A. Anker/Aquatic Invasions)

### 3.23.1 Connectivity

The Kattegat and Øresund are divided into 7 hydrographic regions with intermediate within regions connectivities with coherence values ranging from 44 – 95 %, and with bi-directional connectivity between regions (Figure 29). The central and northern Kattegat consists of 4 hydrographic regions, indicating some limitation in the connectivity across the Kattegat in the east-west direction. Sensitivity analysis carried out for 2005 restricting the larvae dispersal depth to between 0 and 15 meters (Appendix 3) show similar results Dispersal probability plots (Appendix 3) indicate that all major harbors of Kattegat and Øresund (Grenå, Frederikshavn, Varberg, Gothenburg, Copenhagen and Helsingør/Helsingborg) are directly connected (i.e. within 1 generation) to at least one of the other harbors. Some connections between harbors may require more than 1 generation. Dispersal probability in the west- east orientation between Danish and Swedish harbors are predominantly uni-directional towards the east, while dispersal probabilities towards the west is limited, and if considering stepping stone dispersal via multiple generation dispersal probability values are low (< 0.1 %). Harbors of Øresund including Copenhagen, Helsingør and Helsingborg are well connected.

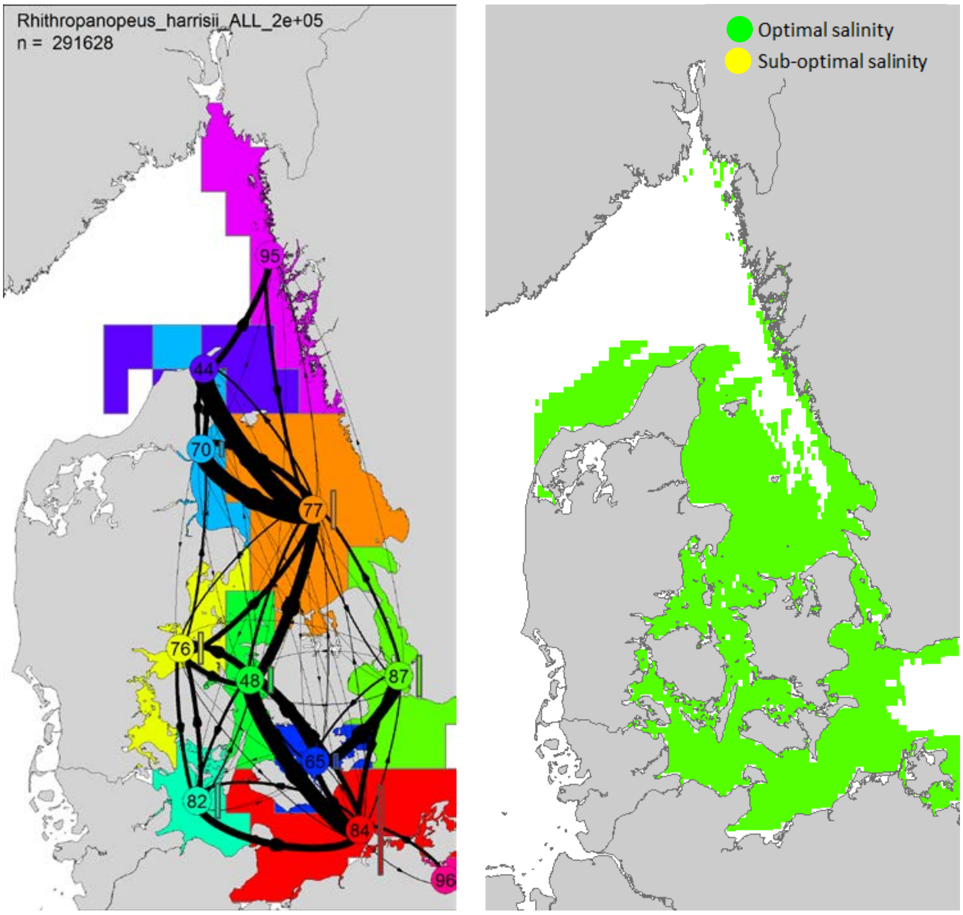


**Figure 29. Left: Hydrographic regions identified for *Rhithropanopeus harrisii* based on 3 years larval dispersal simulation (2005, 2010 and 2012). Right: Predicted habitat based on substrate preferences and salinity tolerance of adult life stages. For detailed description on how to read figures, see methodology section in this appendix.**

### 3.23.2 Robustness of results

In total 291 628 out of 600 000 agents from the 3 years dispersal simulations were included in the connectivity analysis. Very similar results are found for individual years with 2012 showing some indication of a more connected Kattegat from west to east except for the northeastern parts. Sensitivity analysis using different initial numbers of agents (i.e. 50 000 vs. 200 000) per year (Appendix 3) likewise show similar results although with some minor deviations. The results are considered robust.

### 3.23.3 Habitat characteristics

Habitats include all types of substrates down to 37 meters depth. While the species is primarily found in areas with structures providing some kind of shelter including debris, vegetation, stones, biogenic reefs etc. (www.cabi.org) and thus, the habitats included in the larval dispersal and connectivity analysis maybe overestimated and in reality limited to more shallow waters with heterogenic seabed characteristics.  The species tolerate a wide range of salinities with no expected limitations in the Kattegat and Øresund region.

### 3.23.4 Natural Dispersal potential

According to CABI (www.cabi.org), the natural dispersal potential of *R. harrisii* has been discussed since it has been reported that larvae express tidal behavior in tidal estuaries resulting in most larvae settling close to the spawning sites despite reported PLD between 7 to 43 days. In non-tidal or open water parts of the world where the species has been introduced long distance dispersal has been argued to be an important dispersal mechanism also supported by population genetic studies.  The use of 7 days PLD for the Kattegat and Øresund region may be underestimating the dispersal potential and hence the connectivity results. Temperature and salinity conditions are not expected to be a limiting factor for dispersal. According to www.nobanis.org there are a few Danish records from the harbor of Copenhagen and its vicinity in 1954, 1955 and 2008. Recently R. harrisii has become established in southeastern Denmark (Olesen and Tendal 2009).

### 3.23.5 Summary

While the western and eastern parts of the Kattegat and Øresund seem relatively well connected, the connectivity across the Kattegat from east to west may be limited in both the southern and northern parts of Kattegat. Assuming that habitat may be more limited to more heterogenic and structured seabed habitats, this limitation may be even more distinct. On the other hand the PLD may be considerably longer than the 7 days assumed in the larval dispersal simulation with longer PLD favoring more efficient dispersal within the Kattegat. Thus, the connectivity across the Kattegat is somewhat uncertain.

**Table 25. Connectivity ratings and species characteristics for *R. harrisii*. For details on ratings descriptions see methodology section in this appendix.**

| Rhithropanopeus harrisii | | | | | | |
|---|---|---|---|---|---|---|
| Dispersal potential | 2 | | | | | |
| Habitat conditions | 2 | | | | | |
| Pressence status | + | | | | | |
| Robustness | 3 | | | | | |
| Connectivity: | KØ | N | S | W | E | Ø |

| | | | |
|---|---|---|---|
| (red) = No | 1 = Low | - | = Not registered |
| (yellow) = Low | 2 = Medimum | + | = Registered |
| (green) = high | 3 = High | ++ | = Widely distributed |

# 4 Additional data

Previous studies that may support the connectivity patterns observed for Kattegat and Øresund for a number of species in the previous section are limited. Jahnke et al. (2018) published a recent study on population genetics on eelgrass *Zostera marina* in the Kattegat. They studied the genetic similarities and dissimilarities of sub-populations in Kattegat and compared the results with oceanographic analysis of dispersal of passive rafting of flowering shoots which is considered a major dispersal mechanism at this scale, and found that population clusters, barriers and net-works of connectivity were very similar when comparing genetic or oceanographic analyses. Comparisons were best achieved considering multiple generations stepping stone dispersal. Clustering of sub-populations and identification of dispersal barriers found, are similar to the location of dispersal barriers found for a number species in our study. Specifically the location of barriers between the most eastern parts of Kattegat and western Kattegat, a barrier located at the transition zone between Kattegat and Skagerrak, and a barrier located at the farthest south-west corner of Kattegat (all indicated by white hatched lines in Figure 30.

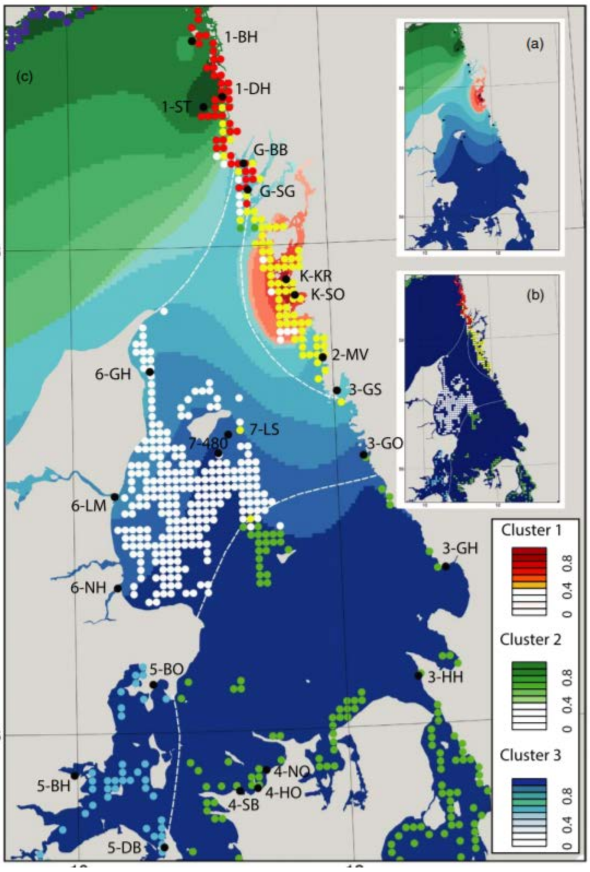


**Figure 30. Dispersal barriers (white hatched lines) identified in Kattegat for the seagrass *Zostera marina* from population genetic studies and multiple generations dispersal modelling (Jahnke et al. 2018).**

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